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THE LARVAL CASE OF *TRIAENODES BICOLOR* CURTIS (TRICHOPTERA : LEPTOCERIDAE)

By A. R. Tindall
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Introduction

Larvae of *Triaenodes bicolor* Curtis were collected from the canal at Kibworth Bridge, Leicestershire (*map ref.* SP 662948) during the spring and early summer of 1959. They were found in considerable numbers amongst masses of *Callitriche* sp. in water between 0·25 and 1 m. deep.

The larvae survived in aquaria so long as they were supplied with sufficient *Callitriche* on which to feed. No aeration was used, and the tanks stood in a sunny window so that the temperature at times rose above 20° C.

Moretti (1942), in a very interesting paper, considers the ecology and feeding of the larvae of *T. bicolor*. He shows that they are destructive pests in the rice-fields of Italy and Japan, where they live in shallow water. He shows, too, that they are tolerant of water temperatures which in summer reach as high as 28° C. at the bottom, and 31° C. at the surface (p. 96).

The Larval Case

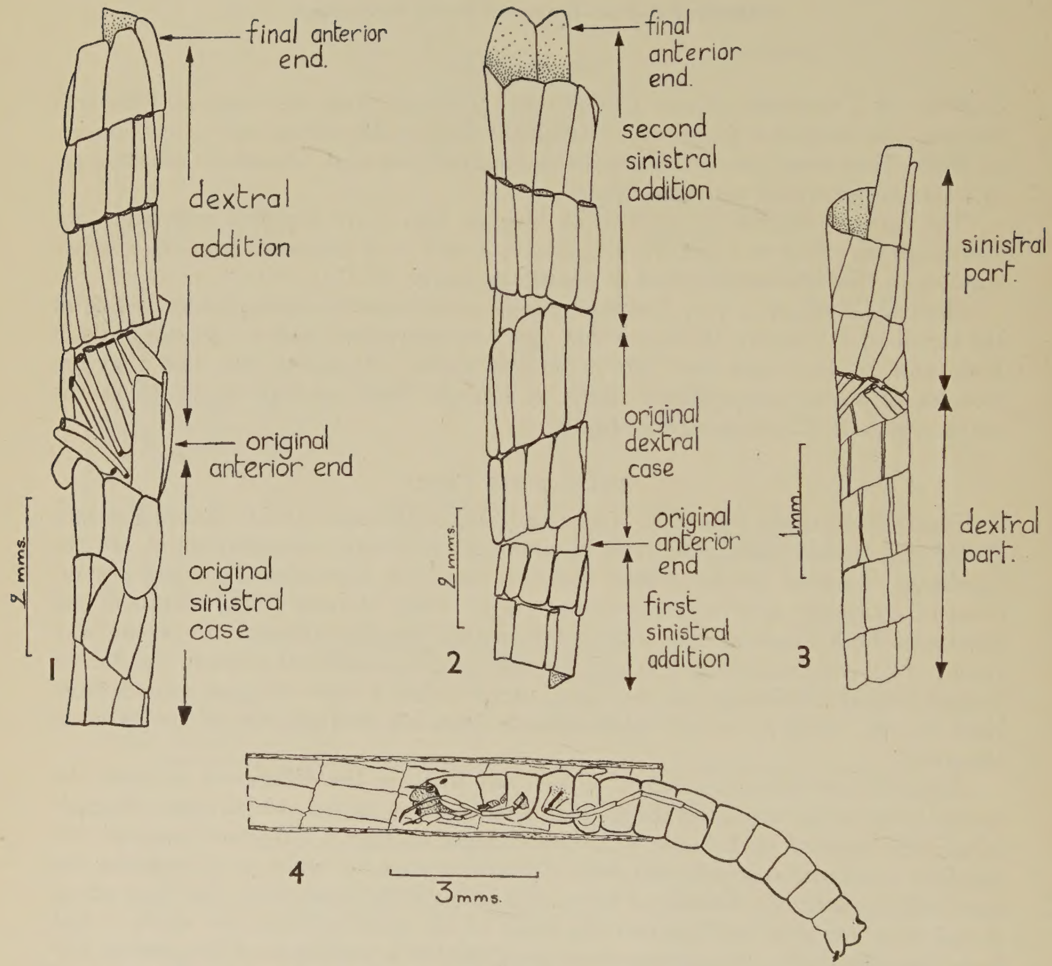
Illustrations of the case of *T. bicolor* are given in Rousseau (1921), Esben-Petersen (1916) and Hickin (1942, 1952), all of whom show it with a sinistral spiral. In the specimens observed by the writer, however, there are approximately equal proportions of sinistrally and dextrally coiled cases. Only Moretti (1942) mentions and illustrates both kinds of case, but unfortunately they are labelled the wrong way round. (To avoid confusion it is pointed out that the definitions given in the *Shorter Oxford English Dictionary* are used here, namely, that a sinistral spiral ascends from right to left, while a dextral spiral ascends from left to right, *i.e.* of the external observer).

Experiments were undertaken to find out whether the differences between the larvae living in the two kinds of case involved structure as well as behaviour. Animals inhabiting cases of both kinds were interchanged so that a " dextral " animal was put into a sinistral case and *vice versa*. The cases were cut short, so stimulating the case-building activity. Usually, a larva built in the same sense as the case from which it had been removed and ignored the sense of the spiral of that into which it had been introduced (fig. 1). In one experiment the larva had reversed its position and added to both ends in the sense opposite to the spiral of the case into which it had been placed (fig. 2). One larva in a collection from the canal was found with a case partly sinistral and partly dextral (fig. 3). So far this is the only example found occurring naturally, in which the case is not purely of one sense.

No structural differences could be found between the larvae of the two kinds of case and it would appear, therefore, that they have a strong tendency to build either sinistrally or dextrally and that this has involved no obvious structural adaptations.

Case Building

This can be very rapid, the larva building approximately 1 cm. of new case in 2 hours, *i.e.* about 30 pieces of weed. In one example, a larva took one minute to bite off a length of stem and two more minutes to attach it on to the end of the case. Either stem or leaf is used, the plant being gripped by the prothoracic legs. The claw



FIGS. 1–4.—*Triaenodes bicolor* Curtis: (1) Sinistral case with a dextral addition by a larva from a dextral case; (2) dextral case with two sinistral additions by a larva from a sinistral case; (3) case, partly sinistral and partly dextral, found in the field; (4) diagram of larva entering case to show disposition of the legs (one half of the case removed).

and tarsus of each leg are flexed towards the femur and enclose the stem or leaf against the distal projection present on the tibia. This action is very similar to that of the louse except that there is no tibial pad in *T. bicolor*. The spines on the inner margin of the femur also help to grip the plant firmly. The leaf, or more especially the stem, is held against the anterior notch of the labrum while the latter is retracted into the head of the larva, and both the mandibles are extended around the stem. The labrum is clearly an important sensory structure, and from observation of the living animals it seems likely that the larva uses the " fit " of the stem in the labral notch to determine its radius or thickness and hence its suitability for case construction.

When a stem proves too tough for the larva to bite through immediately, the mandibles are inserted into it and closed. The tip of the right mandible lies just posterior to the tip of the left, and in the hollow of the latter, thus allowing the tips to overlap. In this position the head of the larva is sharply withdrawn, so snapping the tissues of the stem. This process is repeated until the whole stem is severed.

The larval mandibles of *T. bicolor*, like those of many other species of caddis larvae, are asymmetrical. In *Triaenodes* the left mandible is more elongate and triangular, while the right one is shorter and more rectangular. Various reasons for this asymmetry have been suggested, but the advantage to the *Triaenodes* larva when dealing with tough stem tissues is very obvious. The overlapping of the tips of the mandibles provides a locking device, which, in spite of its simplicity, renders them considerably stronger for tearing tough fibres than mandibles in which the tips just meet. There is a strong parallel to the overlapping canine teeth used for tearing flesh. The inner edge of each mandible is dentate, the teeth interdigitating, and this permits the larva to bite quickly through softer plant tissues such as leaves.

The piece of weed removed is held by the prothoracic legs, whilst the mesothoracic legs grip the anterior end of the case and the metathoracic legs hold on to adjacent plants. The severed weed is held in the correct position while the head moves to and fro across the junction of the new piece and the existing case. The main movement is a close zig-zag along the side and end which touch the existing case, although long movements also occur from anterior to posterior. During these movements silk is produced from the silk glands and laid down in a fine network which binds the new piece of weed to the rest of the case. Microscopic examination of the silk lining shows a very fine irregular reticulation embedded in an amorphous layer, suggesting that there are two components in the thread, namely, the more viscous thread and a more fluid material which coalesces to form a continuous layer. This would explain the adhesion of the plant pieces to the lining and the formation of a coherent case.

At present very little information seems to be available concerning trichopteron silk ; it would be expected to differ from lepidopteron silk, as described by Wigglesworth (1953). Apparently, one element of lepidopteron silk is soluble in water, and, if trichopteron silk were similar, obvious difficulties would arise, since the larvae are aquatic. This is a problem which needs to be investigated further.

Direct observation, confirmed by serial sectioning, shows that the ducts of the paired silk glands fuse to form a common duct immediately posterior to the spinneret. This common duct opens medially on the anterior tip of the labium in a short papillate spinneret.

The maxillary palps are in constant flickering motion throughout the processes of case building, whereas the antennae appear to play little or no part.

Occasionally a larva is seen to protrude the anterior part of its body, and to curve it sharply round, so that its jaws can reach the outside of its case. It appears to be removing algal growth, but it may be attacking epizoites or parasites as well as epiphytes. Sometimes, from this position, the animal leaves its case completely. If this happens, it may enter it again from the anterior end and so finish reversed in position, or from the posterior end and finish in its normal position. In either event, the very long metathoracic swimming legs are pressed closely along the abdomen, as shown in figure 4, while the first and second pairs of legs pull the larva through the case. The larva is also able to reverse its position while remaining inside the case by winding itself into a narrow U-shape, the head and thorax being then dragged past the posterior part of the body, again by the first and second pairs of legs, the third pair trailing behind.

THE PUPAL CASE

The pupal case consists of approximately the anterior 9 cm. of the larval case, with both ends roughly squared off. Contrary to some accounts (Lestage *in* Rousseau, 1921 ; Hickin, 1949), the ends of the pupal case are not plugged with tufts of algal or other plant material, but rather the plant strands, which are present, are attached to the rims of the circular ends of the case, while the ends themselves are covered by discs of tough silk, here termed the end-plates. Further, these are not alike, as is often stated (Klapálek, 1888 ; Moretti, 1942). They are both perforated by a central hole, but the anterior end-plate is more delicate and the hole is circular, while the posterior is more robust with an ovoid hole. The anterior diaphragm is also much flatter than the posterior, which is shaped like a truncated cone pointing posteriorly. This may be to facilitate egress for the water current which is usually passing through the pupal case. It is from the anterior end that the pupa escapes, by breaking the end-plate from the case around approximately half its circumference. Moretti states he has observed pupae in the pupal cases with their heads at the posterior end.

ACKNOWLEDGMENT

These observations were incidental to other studies on this trichopteron, and I wish to express my thanks to Professor H. P. Moon for drawing my attention to it and for his encouragement and patient guidance.

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METHODS OF CASE-BUILDING AND REPAIR BY LARVAE OF CADDIS FLIES

By Hilmy M. Hanna[1]

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Introduction

There have been many experiments on case-building by larvae of caddis flies. Ostwald (1899), Lutz (1930, 1932), Dembowski (1933), Moretti (1934), Fankhauser and Reik (1935) and Dudziak (1950) were concerned to find if caddis larvae would build cases using various unnatural materials. Other published observations on different aspects of case-building have been made by the following workers : Simpson (1903) noted that *Limnephilus indivisus* Walker left their cases and built new ones when sticks used in their construction caused them to float to the surface. Marshall and Vorhies (1905) observed how *Platyphylax designatus* Walker used its mandibles in handling sand grains for case-building and would repair damage done to the anterior end of the case. Bierens de Haan (1922) described *Limnephilus marmoratus* Curtis building a new case. Gorter (1929) made similar observations on *L. flavicornis* (F.). None of these authors described the full sequence of events in case-building. Gorter (1931) gave details of construction of a provisional case followed by a permanent one by larvae of nine species of limnephilids and two species of leptocerids. Dembowski (1933*a*) studied case repair by *Molanna angustata* Curtis, and Teyrovsky (1934) made similar observations on *Neuronia ruficrus* (Scopoli). Copeland and Crowell (1937) studied case-building by *Limnephilus* sp. and *Molanna* sp. Unfortunately these authors did not identify the species. It will be shown later that there is a wide range of behaviour among the different species of *Limnephilus*. Nielsen (1948) studied the case construction of five species of Hydroptilidae. Staropolska and Dembowski (1950) made a further study of the repair of the larval case of *Molanna*. Whitehead (1951) made observations on the increase in size of the larval case of *Limnephilus vittatus* F. Maillet and Carasso (1952) described the case-building of *Triaenodes conspersa* (Rambur). Carasso and Maillet (1954) have also studied case-building by an unidentified species of *Setodes*. Hanna (1957) studied the case-building of *Limnephilus marmoratus* Curtis and *L. politus* McLachlan.

It will be seen, therefore that observations on methods of case construction are scattered and inadequate, and there has been no attempt to make a general survey of the problem. In the present work, representative examples have been studied from all families in which larvae that build portable cases occur, except the Hydroptilidae, of which a detailed study has already been made (Nielsen, 1948).

Material and Methods

The species studied are listed in Table I. The localities where they were collected are mentioned in an unpublished thesis (Hanna, 1956). The classification adopted is that used by Mosely (1939) with alterations in generic names suggested by Kimmins (1942, 1952, 1956).

The larvae were pushed out of their cases and supplied with their natural case-building material. They were observed under a binocular microscope and the sequence of building activity recorded. The stream forms were observed in a small chamber designed by the author for this purpose (Hanna, 1956).

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Experiments were also carried out on the growth of the case. Quick-drying paint was used to mark the posterior end so that it would be recognised if cut off. The same paint was sometimes used to mark the anterior end so that the addition of new material could be detected. Contrasting materials, such as chips of porcelain or red brick for larvae constructing sand grain cases, were also supplied so that it was easy to detect the new material.

Other experiments were also made to study the repair of the case after the anterior or posterior end had been damaged.

In each of the experiments a large number of larvae belonging to all stages were examined. The majority were reared to the adult stage.

RESULTS

The larvae studied employ the following eight main methods of starting their cases.

(1) *The tunnel method.*—The larva secreted silk over a heap of dead leaves which it had collected with the claws of the pro- and mesothoracic legs. It crawled under the heap and drew beneath itself a dead leaf, which was held in the angle of the femora and tibiae of the pro- and mesothoracic legs, and then joined the heap of material first collected to this leaf to form a tunnel (fig. 1). This method was typical for *Trichostegia minor* (Curt.). In the other species which practised this method, the tunnel was as long as the abdomen and it was only provided with a floor at its anterior end.

(2) *Dorsal plate method.*—The larva lay on its back and picked up pieces of leaves with the pro- and mesothoracic legs. Many leaves were collected in this way and pushed backwards with the metathoracic legs and then joined with silk to form a plate over the abdomen. At the anterior end of this plate a square was then built round the thorax by first fixing a leaf to the anterior end of the plate with silk secretion and then adding one to each side and to the ventral surface, thus forming a square (fig. 2).

In *Glyphotaelius pellucidus* (Retzius) the dorsal plate was built differently. The larva crawled among the dead leaves and joined two or three to form a plate over the abdomen. A square of dead leaves was then built anterior to this dorsal plate, a large leaf fixed at right angles to it and a second leaf to the other side. The larva then fixed a small piece of leaf to the ventral and to the dorsal surfaces (fig. 3).

In *Chaetopteryx villosa* (F.) the dorsal plate was short and covered only a small part of the abdomen. In this species and in *Molanna angustata* the dorsal plate was built of grains of sand.

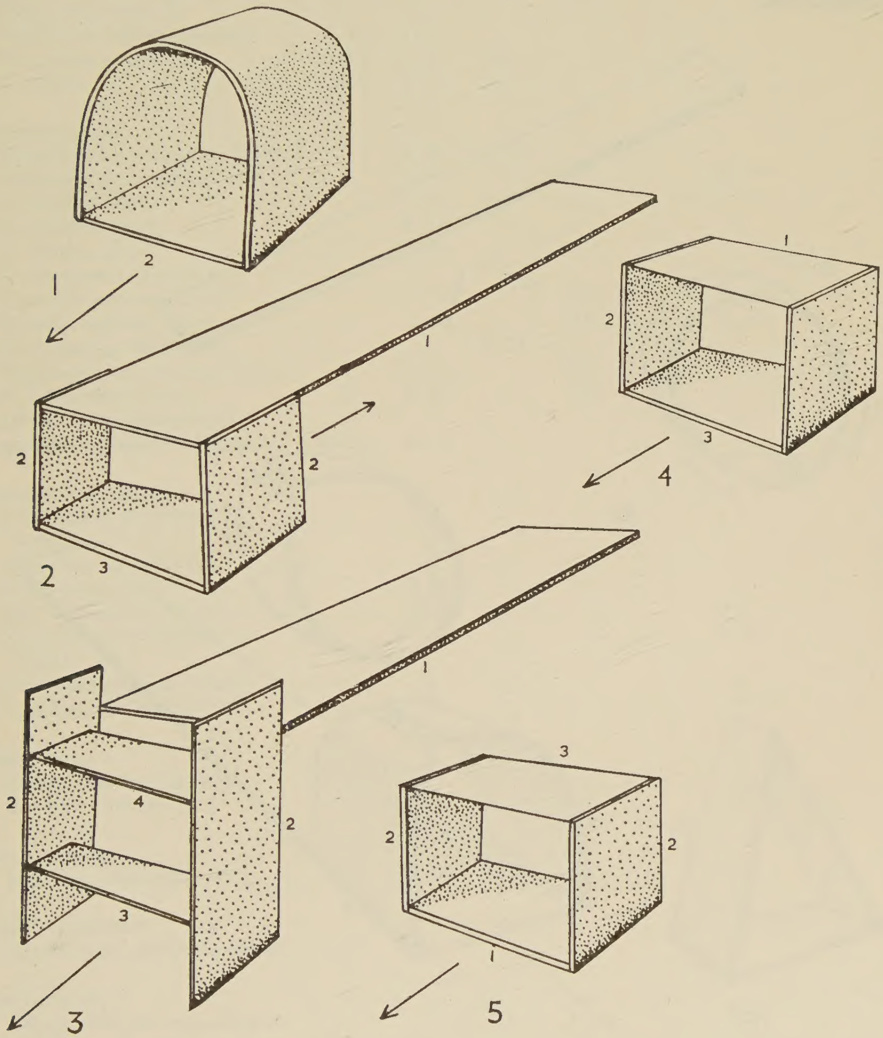
(3) *The ventral plate method.*—I have already described this method in a previous paper (1957).

(4) *The square method.*—The larva built an initial plate in the way already described in the tunnel method. It then crawled under the heap and built a square by adding material to each side and to the ventral surface (fig. 4). Many larvae, however, crawled over the heap and added material at each side and then to the dorsal surface (fig. 5).

(5) *The belt method.*—The larva secreted silk over a heap of the material provided and which it had collected with the claws of the pro- and mesothoracic legs. It then crawled over the heap, lay on its back and pulled the two ends together with the claws of the mesothoracic legs and joined them with silk. Many larvae, however, crawled under the heap and joined the two ends ventrally. The two ways of forming the belt are shown in figure 6. When the larvae of *Beraeodes minuta* (L.), *Athripsodes aterrima* (Stephens) and *Triaenodes bicolor* (Curt.) failed to join the two ends together to form the belt, they fixed the plate to the sternum of the first abdominal segment by silk threads. The abdomen was then bent forwards under the thorax until the

anal claws reached the plate and its end was then moved sideways in a dorsal direction a few times until the plate had been transferred to the side of the thorax. The plate was long enough to hang on both sides of the thorax. The prothoracic legs pulled the two ends together and joined them with silk secretion to form a belt.

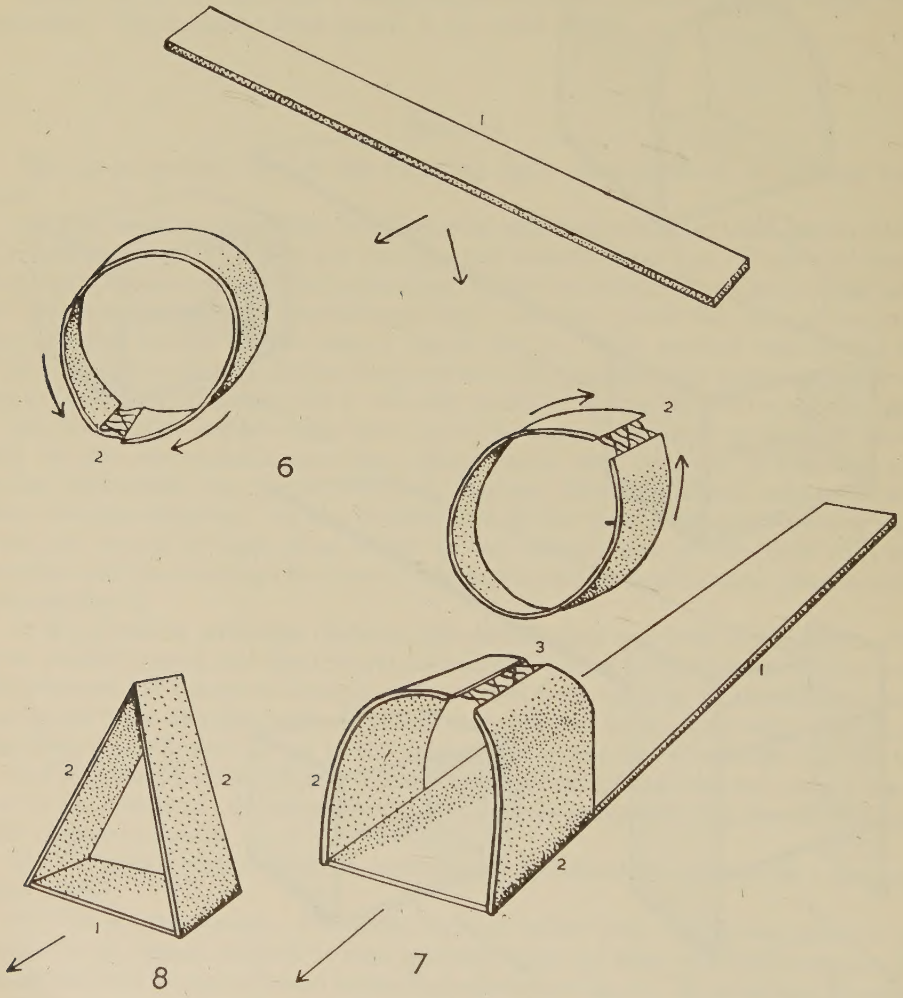
(6) *The T method.*—The caseless larva secreted silk over a heap of sand grains and small stones, which it had collected by the claws of the pro- and mesothoracic legs. Sand and small stones were then added first to one side of the heap and then to the other to form a T-shaped structure. The larva then lay on its back, pulled the two ends of the cross plate together with the mesothoracic legs and joined them with silk (fig. 7).



Figs. 1–5.—Diagrams showing the construction of: (1) a tunnel by larvae of *Trichostegia minor* (Curt.); (2) a dorsal plate and a square by larvae of *Agrypnia pagetana* Curt.; (3) the foundation of the case by larvae of *Glyphotaelius pellucidus* (Retz.); (4) a square by larvae of *Phryganea varia* F.; (5) a square by larvae of *Oligotricha ruficrus* (Scop.).

(7) *The burrowing method.*—The larva burrowed into the sand using the pro- and mesothoracic legs. The head and thorax penetrated gradually, whereas the abdomen

was nearly vertical on the substratum. The larva then stopped burrowing for about 20 minutes, during which the abdomen rotated slowly. When some of the larvae were taken out at this stage, a ring of sand grains and small stones had been built round the thorax. They continued to burrow until they were completely buried. Examination of the cases at this stage showed that the larvae had built a loose case of sand grains of varying size. They then constructed a definitive case in front of the provisional one.



Figs. 6–8.—Diagrams showing the construction of: (6) a belt by larvae of *Limnephilus flavicornis* (F.) and *L. lunatus* Curt.; (7) the foundation of the case by larvae of *Limnephilus fuscicornis* (Ramb.); (8) a triangle by larvae of *Glossosoma boltoni* Curt.

(8) *The triangle method.*—The larva anchored itself by the anal claws on a small stone. A small stone was then fixed to the sterna of the meso- and metathorax and a further stone obliquely to each side of these segments, thus completing a triangle (fig. 8). The larva then proceeded to build the anterior part of its case in front of this girdle by fixing stones to the sides and then constructing the floor. When the anterior part was completed the larva reversed itself inside the case, cut away the triangle at the posterior end, thus completing a normal case.

The distribution of the eight methods in various species is recorded in Table I.

TABLE I.—*Distribution of methods of case building by larvae of Caddis flies*

Species studied	Tunnel	Square	Dorsal plate	Ventral plate	Triangle	Belt	T	Burrowing
PHRYGANEIDAE								
Trichostegia minor (Curt.)	Y, O	.	.	.	.	.	.	.
Agrypnia pagetana Curt.	.	.	Y, O	.	.	.	.	.
Phryganea varia F.	O	Y	.	.	.	.	.	.
Oligotricha ruficrus (Scop.)	Y, O	Y, O	.	.	.	.	.	.
Phryganea grandis L.	Y, (O)	Y, O	(O)	.	.	.	.	.
P. striata L.	Y, (O)	Y, O	(O)	.	.	Y	.	.
LIMNEPHILIDAE								
Glyphotaelius pellucidus (Retz.)	.	Y, O	Y, O	.	.	.	.	.
Limnephilus flavicornis (F.)	.	Y, O	.	.	.	Y, O	.	.
L. lunatus Curt.	.	Y, O	.	.	.	Y, O	.	.
L. centralis Curt.	.	Y, O	.	.	.	.	.	.
L. vittatus (F.)	.	Y, O	.	.	.	.	.	.
L. fuscicornis (Ramb.)	.	.	.	.	.	.	Y, O	.
Anabolia nervosa (Curt.)	.	.	.	(O)	.	Y, O	.	.
Halesus radiatus (Curt.)	.	.	.	(O)	.	Y, O	.	.
Chaetopteryx villosa (F.)	.	.	Y, O	.	.	.	.	.
Potamophylax stellatus (Curt.)	Y	Y, O	.	(O)	.	.	.	.
P. latipennis (Curt.)	Y	Y, O	.	(O)	.	.	.	.
Drusus annulatus Steph.	.	.	.	.	.	.	.	Y, O
Apatania muliebris McLachl.	.	Y, O	.	.	.	.	.	(Y)
SERICOSTOMATIDAE								
Sericostoma personatum (Spence)	.	.	.	.	.	.	.	Y, O
Notidobia ciliaris (L.)	.	.	.	.	.	.	.	Y, O
Goëra pilosa (F.)	.	Y, O	.	.	.	.	.	.
Silo nigricornis (Pictet)	.	Y, O	.	.	.	.	.	.
Brachycentrus subnubilus Curt.	.	.	.	.	.	Y, O	.	.
Crunoecia irrorata (Curt.)	.	Y	O	.	.	.	.	.
Lepidostoma hirtum (F.)	.	Y	.	.	.	O	.	.
BERAEIDAE								
Beraea maurus (Curt.)	.	Y	.	.	.	.	.	.
Beraeodes minuta (L.)	.	.	.	.	.	Y	.	.
MOLANNIDAE								
Molanna angustata Curt.	(Y)	(Y, O)	Y, O	.	.	.	.	.
ODONTOCERIDAE								
Odontocerum albicorne (Scop.)	.	.	.	.	.	.	.	Y, O
LEPTOCERIDAE								
Athripsodes aterrima (Steph.)	.	.	.	.	.	Y, O	.	.
A. cinerea (Curt.)	.	.	.	.	.	.	.	Y, O
Oecetis lacustris (Pictet)	.	.	.	.	.	.	.	Y, O
Mystacides nigra (L.)	.	.	.	.	.	Y, O	.	.
M. longicornis (L.)	.	.	.	.	.	Y, O	.	.
Triaenodes bicolor (Curt.)	.	.	.	.	.	Y, O	.	.
RHYACOPHILIDAE								
Agapetus fuscipes Curt.	.	Y, O	.	.	.	.	.	.
Glossosoma boltoni Curt.	.	.	.	.	Y, O	.	.	.

Y = Young larvae.
O = Old larvae.
( ) = Uncommon.

Reconstruction of the Provisional and Definitive Cases

The larvae examined normally built a loose provisional case in front of the preliminary structure. The species which live in cases of sand grains do not appear to select their material for the provisional case, as grains of varying sizes are used. Of those species which use plant materials, the larvae of *Trichostegia minor*, *Agrypnia pagetana*, *Glyphotaelius pellucidus*, *Brachycentrus subnubilus* and *Triaenodes bicolor* select certain materials at all stages of case construction. Furthermore, in *A. pagetana* the larvae cut the material into pieces of suitable size. The other species did not show any preference for any particular material in building the provisional case. When the latter was completed the larva started to build the definitive case in front of it. When the case was as long as the abdomen, the larva reversed itself and cut off the provisional case with the mandibles, pushing it away with the legs. The larva then returned to its normal position and continued to add to the case at the anterior end. From time to time it reversed itself to secrete silk inside the case. The selection of materials for building the definitive case will be considered in a future paper.

Growth of the Case

Increased size of the case was achieved in one of two ways:

(a) *Addition at the anterior end and cutting of the posterior end.*—This was the method found in all species studied except *Agapetus fuscipes*, *Glossosoma boltoni* and *Agrypnia pagetana*, which inhabited empty stems. Cutting the posterior end is essential, because it becomes too narrow for the growing larva. In cases built of plant material, this part becomes rotten, which may be an additional reason for cutting it away. McLachlan (1864) observed many *Phryganea* larvae doing the same.

According to Struck (1900) and Silfvenius (1902), the larva of *Stenophylax nigricornis* Pictet partially closed the anterior end and then added to the former posterior end. They regarded this as normal for this species. I have seen the same procedure, as an abnormality, in a few specimens of *Limnephilus lunatus* and *Chaetopteryx villosa*.

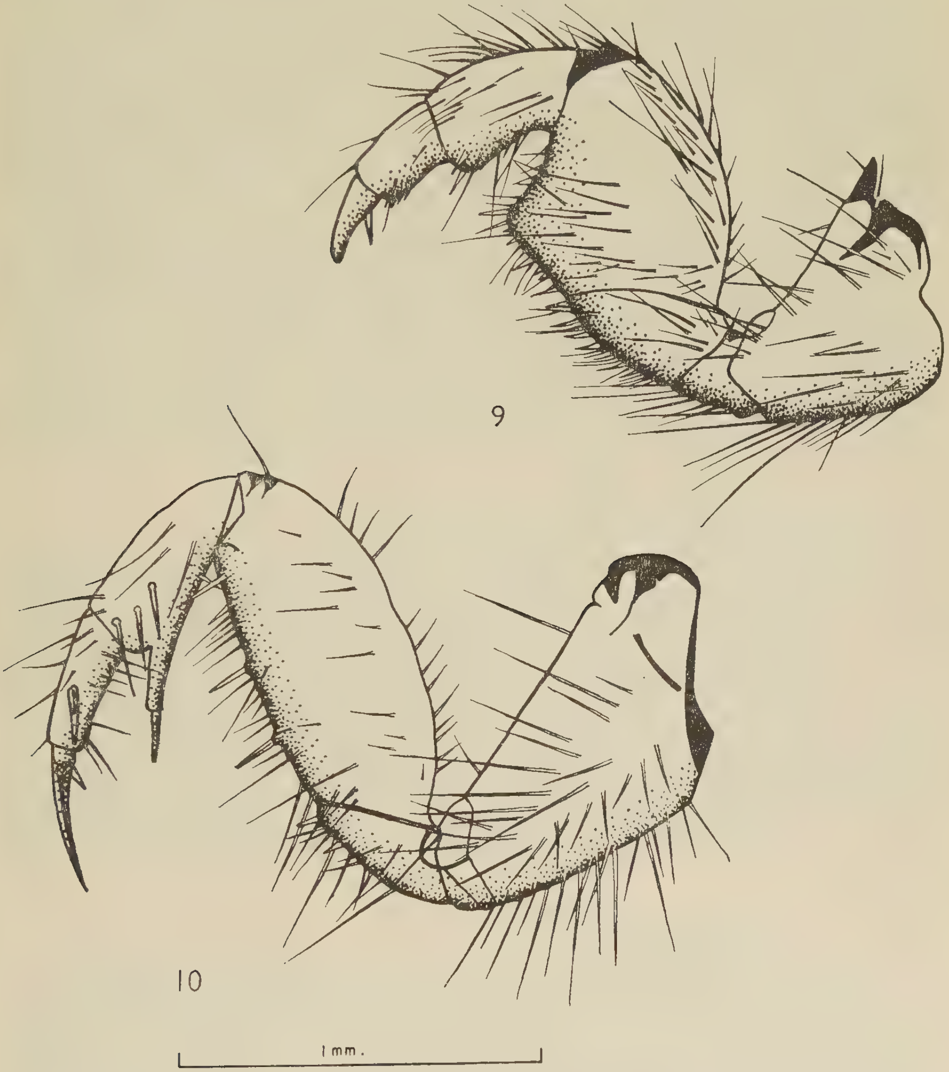
(b) *Leaving the case.*—The larvae of *Agrypnia pagetana*, which inhabit empty stems, left their cases and sought others as they grew. These observations agree with those of Struck (1899, 1900). The larvae of *A. fuscipes* and *G. boltoni* left their cases and built new ones as they grew.

Repair of the Cases

When the posterior end of the case was damaged the larvae of Phryganeidae, and of *P. stellatus*, *P. latipennis*, *C. villosa*, *A. fuscipes* and *G. boltoni* repaired it by adding material mainly at this end. The cases of these species are wide enough to allow the larvae to reverse themselves easily. In other species little or no material was added to the posterior end. Holes in the cases of Phryganeidae and Rhyacophilidae were repaired with a film of silk applied on the inside. In all other families the posterior holes were usually neglected. All the species studied were seen to touch the holes with the labium, maxillary palps and prothoracic legs before starting to repair them, presumably to explore the extent of the damage.

DISCUSSION

From the above observations it appears that the larvae studied employ eight main methods of starting a case. These methods can be grouped as follows: *The square, dorsal* and *ventral plate methods* are basically similar. In all three the larvae add material at right angles to an initial plate and then a roof or a floor is built. In the square method this initial plate is short, whereas it is long in the other two. *The triangle method* is also comparable with these three methods but the material is added obliquely to each side, so that there is no need for a final roofing plate. *The belt* and *T methods* may be considered together. Instead of adding material to the sides and to the roof, the belt or T is pulled round the larva and the two ends joined with silk. *The tunnel method* appears to differ from all the others. The initial plate overhangs the larva on both sides and then material is added ventrally to form a floor for the tunnel. *The burrowing method* also differs, since the larva burrows into the sand, joining grains together into a case.



Figs. 9–10.—Prothoracic leg (posterior view) of: (9) *Sericostoma personatum* (Spence); (10) *Molanna angustata* Curt.

The T and ventral plate methods were restricted to the Limnephilidae, and the triangle method to the Rhyacophilidae. The other methods were found in more than one family. There were 23 species which used one method only, ten species used two, four species three and a single species used four methods.

The material used in the construction of the case is gathered and manipulated by the legs: it might therefore be expected that these would show adaptations for this activity. In the species observed there appear to be the following different ways of holding the material while incorporating it into the case.

(*a*) By the claws of the pro- and mesothoracic legs (*D. annulatus*, *A. muliebris*, *G. pilosa*, *S. nigricornis*, *A. fuscipes* and *G. boltoni*). There appear to be no special modifications of the legs.

(*b*) In the angle between the femora and tibiae of the prothoracic legs and by the claws of the mesothoracic legs (*G. pellucidus*, *L. flavicornis*, *L. lunatus*, *A. nervosa*, *H. radiatus*, *P. stellatus*, *P. latipennis*, *C. villosa*, *B. subnubilus*, *C. irrorata* and *L. hirtum* and the leptocerids). The inner surface of the prothoracic femora is convex, which may be an adaptive feature for holding the material.

(*c*) In the angle of the femora and tibiae of both pro- and mesothoracic legs (Phryganeidae). The inner surface of both pro- and mesothoracic legs is convex.

(*d*) Between the process of the femora and the tarsal claws of the prothoracic legs (*S. personatum* and *N. ciliaris*). The femur of each prothoracic leg has a well-developed process on its inner surface which appears to be a special development for holding sand grains (fig. 9).

(*e*) In the pincer-like structure formed by the tibial spur and the tarsal claw of the prothoracic legs (*M. angustata*). The tibial spur of the prothoracic leg is situated on a prolongation of the tibia which is longer than the spur itself; this seems to be an adaptive feature for holding sand grains (fig. 10).

In *L. centralis*, *L. vittatus*, *L. fuscicornis*, *B. maurus*, *B. minuta* and *O. albicorne*, the method of holding a sand grain seems to depend on its size; fine grains are held with the claws of the prothoracic legs, while large ones are held in the angle of the femora and tibiae of these legs.

A Comparison of Original and Reconstructed Cases

The fully-grown larvae which normally live in curved tapered cases always rebuilt cylindrical cases with no evidence of tapering, but the curvature was gradually achieved. It appears, therefore, that tapering is the normal result of the growth of the larva, as has been suggested by Maillet and Carasso (1952) for *Triaenodes conspersa*. Curvature, on the other hand, is a result of the way in which the larva of any age adds material, as I have confirmed from observations on many species. A larva which cuts away only a small amount of the posterior end of its case produces one which is markedly tapered, whereas if a lot of material is cut away, the case is only slightly tapered or cylindrical. The reconstructed cases of *A. fuscipes* and *G. boltoni* are similar to normal ones because in nature the larvae apparently leave their cases and build new ones as they grow. The shape of the case is, therefore, not the result of growth.

Origin and Loss of Building Instinct

Milne and Milne (1939) suggested that the ancestral caddis larvae occupied silken galleries in ponds and streams. Because of food preferences and the general difficulty of maintaining a respiratory current, the Rhyacophilidae left their shelters and moved upstream, actively hunting their prey. Other carnivores also moved upstream but made their shelters in the form of loose structures on rock surfaces. They relied on water currents to bring food and some groups then constructed nets to increase the catch. The vegetarians and scavengers reinforced the walls of the gallery, shortened it and separated it from the substratum. Thus the portable case was evolved. Betten (1934) and Nielsen (1948) both suggested that case-building may have originated from building a pupal shelter. Nielsen then explained the construction of the larval case as a shifting back in time of behaviour because of the case-building instinct.

From my observations on methods of case-building it appears that the burrowing method is less evolved than the others. The larva simply burrows into the sand, joining grains together into a case, and it is reasonable to suggest that case-building may have evolved from a burrowing habit. The hypothetical ancestral caddis larva might then have come to the surface of the sand owing to lack of food or oxygen and built a fixed tunnel to protect it from predators. The final stage would then have been the flooring of the tunnel and its separation from the substratum to form a portable case.

Young larvae built their cases quickly, and appeared to be continuously active during all stages of construction. Older larvae exhibited periods of inactivity, which lasted up to one hour, depending on the species. These periods of inactivity usually increased in number and were longer in fully-grown larvae. That this is not due to lack of silk is shown by the fact that larvae of the Phryganeidae, Limnephilidae, Sericostomatidae, Molannidae and Rhyacophilidae, when pushed out of their partly rebuilt cases during a period of inactivity, started to built new cases immediately. Many fully-grown larvae of *S. personatum*, *N. ciliaris*, *G. pilosa*, *S. nigricornis* and *O. albicorne* failed to build new cases and eventually died if they were not supplied with portions of their cases. All fully-grown larvae of *B. maurus* and *B. minuta* failed to build new cases or to repair their original cases. In the species studied the larvae which had stopped feeding in preparation for pupation failed to construct new cases. All these observations suggest that there is a tendency to lose the instinct for building a portable case as the larva grows older. Gorter (1931) suggested that there was a temporary reduction of the building instinct during the construction of the provisional case, which is usually built quickly, the material having no special arrangement. In my opinion the purpose of building a provisional case is simply to form a protective sheath round the soft abdomen as quickly as possible. Once the larva has done so, the definite style of the case soon appears. There need not, therefore, be any loss of the building instinct in building the provisional case. Uhlmann (1932) suggested that case-building is reduced in older larvae of *Brachycentrus* and in the larvae of all stages of *Setodes*, since the cases are built of silk only. He further suggested that in all species the building instinct is reduced prior to pupation, when silk only is used to close the case. In all cases, however, whatever substances may be used, silk is always secreted in large quantities as part of the building process. I cannot, therefore, agree that these species which build of silk only have lost the building instinct. Moretti (1934) found that when caseless larvae of *G. pellucidus*, *L. rhombicus* and *S. personatum* were kept for a long time without material, they became incapable of building a protective case when material was again available. This observation is interesting but does not contribute to an understanding of the normal loss of the building instinct.

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THE EVOLUTION OF SPERMATOPHORES IN INSECTS

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1. Introduction and Acknowledgments

The spermatophore is commonly regarded as a container which serves to protect the semen during the transfer from the male to the female, but the discovery that in some insects the spermatophore functions as a sperm plug to hold the semen in the bursa copulatrix of the female until it is transported to the spermathecae (Davey, 1958) raises certain questions. One intriguing problem concerns the origin and evolution of this type of semen transfer and its relation to processes involving more typical spermatophores. On the other hand, a number of insects do not form spermatophores, but transfer free sperm to the female. The relationship between this form of copulation and spermatophore formation is also of interest.

Khalifa (1948, 1949*b*) has already examined these problems, concluding that the ancestors of insects developed the spermatophore habit as an adaptation to a terrestrial environment and that the development of direct semen transfer involved the loss of the spermatophore. He was unable to offer any satisfactory explanation for the apparently sporadic distribution of the two forms of semen transfer among the insects. More recently, Ghilarov (1958) has studied the evolution of the two modes of insemination in various terrestrial arthropods and he concludes that spermatophore formation is a primitive character and that forms delivering free semen developed from spermatophore-producing individuals.

The present work consists of a review of the pertinent literature and re-examines the phylogenetic origin and present distribution of the two methods of semen transfer in insects.

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2. Reproduction in the Insect Ancestor

Tiegs (1940) presents evidence that insects are descended from an aquatic Onychophora-like ancestor which shed its semen into the water, and Khalifa (1949*b*) suggests that the spermatophore rose as an adaptation to a terrestrial environment. He considers that the condition in the Onychophoron *Peripatopsis*, in which the spermatophores are placed on the body surface and the spermatozoa pass through the body wall into the haemocoel (Manton, 1938), represents a crude attempt to achieve internal fertilization and is an early step in the development of the modern spermatophore habit.

Other members of the Onychophora, however, produce more typical spermatophores. Ceréonot (1949) describes a flask-shaped spermatophore in which the neck of the flask penetrates into the genital aperture of the female, but the bulb remains outside. The semen, contained in a sperm sac in the bulb, migrates to the spermatheca via a channel in the neck of the spermatophore.

We may now consider semen transfer in certain aquatic Crustacea. Many of these animals produce a spermatophore which is fastened to the ventral surface near the genital aperture (Lloyd and Yonge, 1947 ; Matthews, 1954). The spermatophore then functions as a storage vessel until the spermatozoa are shed into the water with the eggs. This spermatophore, also consisting of a sperm sac in a gelatinous matrix, is obviously not an adaptation to a terrestrial environment, but a means of ensuring a ready supply of semen for the ripe eggs. While it is not suggested that the spermatophores of insects and crustaceans are homologous (although this may be so), it is possible that the primitive aquatic ancestor of insects already possessed a spermatophore which functioned in a similar way to the crustacean spermatophore. The emergence from the water on to the land, then, was marked not by the development of a new structure, but by the extension of the already existing spermatophore into the genital ducts of the female, thereby achieving internal fertilization. That exactly this method of semen transfer exists in some Onychophora, the closest living relative of the insect ancestor, adds weight to the argument.

Other Onychophora, notably members of the genus *Paraperipatus*, do not produce spermatophores, but place the semen directly into the spermatheca by means of the intromittent organ (Ceréonot, 1949). It is significant, however, that the accessory glands associated with spermatophore production are present in *Paraperipatus*, but in a reduced form, indicating that the spermatophore habit preceded the direct transfer of semen.

Within the Onychophora we can see three methods of achieving internal fertilization, a necessary prerequisite for life on land : (1) the extension of the existing spermatophore into the female ducts by means of a long neck ; (2) the loss of the spermatophore and deposition of free spermatozoa in the spermathecae ; and (3) the placing of spermatophores on the body surface and the penetration of the semen into the haemocoel. The last method does not appear to have been wholly successful, but the other two developments are encountered again and again among the insects. With this background in mind, a brief survey of the methods of semen transfer in the various major groups of insects may be illuminating.

3. The Apterygota

Information concerning the reproductive processes in the apterygote insects is so scarce that it is impossible to say more than that spermatophore-like structures are formed in some species. Schaller (1952 ; 1953) has described a structure in the Collembola consisting of a sperm sac containing the semen on the end of a hyaline stalk. This stalked structure is placed upright on the ground by the male and the female later moves over the stalk, inserting the sperm sac into her own genital aperture.

A similar sort of behaviour has been observed in the Thysanuran *Thermobia* (Sweetman, 1934), and Sturm (1952) noted that the male of *Machilis* presents the female with a series of sperm droplets strung on a long hyaline stalk. Whether or not there are accessory glands associated with the production of these spermatophores is uncertain. Information about the Protura and Diplura is totally lacking.

4. The Orthopteroid Orders

Among the remaining insect orders, one pattern of spermatophore structure prevails. As in the Onychophora, there is a gelatinous matrix containing one to several sperm sacs. Where the spermatophore is exposed, the gelatinous matrix may be covered by a tough membranous outer layer. There may be elaborations on this plan, as in the complex spermatophore of *Gryllus* (Khalifa, 1949*a*), but these are not common. More frequently the spermatophore has been simplified by the reduction or loss of one or more of these components. In *Rhodnius*, for example, only the gelatinous matrix remains, the sperm sacs having disappeared (Davey, 1959).

The orthopteroid orders present a good example of progressive specialization of the spermatophore. Of the species that have been examined, all possess a spermatophore, although, as we shall see, it may be considerably modified. Chopard (1934) and LeFeuvre (1939) have reported spermatophores in the Phasmida in which a gelatinous bulb containing the sperm sacs remains outside the genital opening and a short neck penetrates into the ducts, recalling the condition in some Onychophora.

In the Dictyoptera, the Mantidae possess a similar spermatophore, but the subgenital plates of the female are modified to conceal the spermatophore (Roeder, 1935), thus protecting it from being eaten by other insects, a fate which has been recorded for the spermatophore of phasmids (LeFeuvre, 1939). The cockroaches also possess spermatophores consisting of sperm sacs in a gelatinous matrix, but there is no neck, the sperm sacs establishing direct connection with the spermatheca (Gupta, 1947; Khalifa, 1950*c*; Roth and Willis, 1954). The tendency to concealment of the spermatophore is continued in the cockroaches and the subgenital plates are modified to hide it completely.

In the Orthoptera a trend in a different direction is apparent. While the Tettigoniidae (Khalifa, 1949*b*) and the Gryllidae (Khalifa, 1949*a*) possess a spermatophore like that in the Phasmida, the Acridiidae have so reduced the spermatophore that the gelatinous matrix is lacking and the sperm sac is simply a temporary extension of the penis penetrating to the spermatheca (Uvarov, 1928; Khalifa, 1949*b*).

Information concerning the other orthopteroid orders is lacking, but it is clear that on the one hand the spermatophore is retained in its original form but becomes more and more an internal structure in the female, while, on the other hand, the gelatinous matrix has been reduced, leaving only the membranous sperm sac. Here, then, is a structure, which, as we have seen, was originally a means of protecting the spermatozoa until they were used in fertilization, but which is now primarily concerned with the transport of the semen to the spermatheca. In establishing internal fertilization, these insects have taken advantage of the possession of the spermatophore which has been modified to fulfill a new function.

5. The Hemipteroid Orders

The reproductive processes of the hemipteroid orders have not been extensively studied, but among the Heteroptera the spermatophore of *Rhodnius* has been the subject of a good deal of research (Khalifa, 1950*a*; Davey, 1959). It is clear that the spermatophore in *Rhodnius* is a gelatinous mass composed of a mucroprotein secretion originating in the accessory glands of the male and solidifying in the more acid environment of the intromittent organ. Further, the spermatophore, which is contained in the female in the bursa copulatrix appears to function as a sperm plug, holding the semen in place until it is sucked into the spermathecae by contractions of the female ducts (Davey, 1959). In this case, the spermatophore has been retained in a reduced form with the sperm sacs lacking.

Another trend in the Heteroptera is exemplified by *Oncopeltus*, in which the reproductive processes have been so elegantly investigated by Bonhag and Wick (1953). In this species the semen is deposited directly in the spermatheca by the long flagellar intromittent organ. The spermatophore is absent in *Oncopeltus*, but the accessory glands are present as the apparently functionless mesadenes, the secretion of which has been found to have many histochemical properties in common with the secretion of the glands in *Rhodnius*. This evidence supports the view that the spermatophore is a primitive character and that forms delivering free semen evolved from spermatophore-forming forms.

The remainder of the hemipteroid orders are very poorly documented. Some Psocoptera produce a spermatophore which is inserted directly into the spermatheca and remains there throughout the life of the female (Finlayson, 1948), and Khalifa (1949*b*) suggests that the Mallophaga may effect the transfer of semen in a similar fashion. Among the Homoptera, Strübung (1954) has described a spermatophore in the Fulgoridae.

6. The Panorpoid Orders

The panorpoid complex is composed of five phylogenetically related orders: it is considered that the primitive Mecoptera gave rise to the Diptera on one hand, and the Lepidoptera-Trichoptera on the other, with the Neuroptera forming a more distantly related group (Imms, 1957). There is a marked dichotomy in the methods of semen transfer within the complex, which, as we shall see, follows the phylogenetic relationships.

Since spermatophores are not mentioned in studies on the peculiar mating habits of the Mecoptera (Grassé, 1951), it is probably safe to assume that this order does not form spermatophores. Accessory glands are present in the males of all of the families studied by Potter (1938), indicating that the ancestors of the Mecoptera probably formed spermatophores. The females of these families are remarkable in the possession of a very long spermathecal duct, and the male genitalia show a gradation from a sac-like penis with a terminal gonopore in the Boreidae to a long flagellum in the Bittacidae. No observations on the relationship of the parts during mating are available, but it is likely that in the Boreidae the sac-like penis fills the bursa and the terminal gonopore is in a position opposite the entrance to the spermathecal duct; in the remaining families a papilla or flagellum would penetrate a greater or lesser distance into the duct. The Mecoptera appear to have lost the spermatophore early in their phylogeny and have tended to develop a flagellar penis to transport the semen to the spermatheca. Their close relatives, the Diptera, do not form spermatophores (Khalifa, 1949*b*).

The Lepidoptera, on the other hand, appear to have separated from the ancestral stem rather earlier, for they exhibit a remarkable homogeneity in the other direction. A number of authors have described spermatophores in the Lepidoptera (Norris, 1932; Hewer, 1934; Musgrave, 1937) and Khalifa (1950*b*) suggests that all members of the order are spermatophore producers. All of these spermatophores consist of one or more sperm sacs embedded in a gelatinous matrix and are placed in the bursa copulatrix of the female, where the spermatophore appears to act as a sperm plug during the complex migration of the spermatozoa to the spermatheca.

The Trichoptera present a less uniform appearance. Some families, notably the Sericostomatidae, Molannidae and Limnophilidae, produce a typical spermatophore like the Lepidoptera, while others (Leptoceridae, Polycentropidae and Psychomyidae) deposit free sperm directly into the spermatheca (Khalifa, 1950*b*). Deoras (1944), in his examination of the morphology of the reproductive organs of the Trichoptera, appeared to be unaware of the existence of spermatophores in the group, but recognised a dichotomy in the morphology of the male system. In one group, including the spermatophore-forming families of Khalifa, the accessory glands were very prominent and the penis was "directed upwards". In the other, including those families which delivered free semen, the accessory glands were reduced and the penis was "directed downwards". It is difficult to be certain about the details of the differences in the external genitalia, but it is clear that those families which deliver free sperms nevertheless retain the accessory glands in a reduced form.

The remaining panorpoid order, the Neuroptera, have retained the spermatophore in a fairly primitive form, which is reminiscent of the Onychophora. It consists of a flask-shaped gelatinous matrix containing two sperm sacs, with the bulb of the flask remaining outside the female and the neck penetrating into the ducts. In *Osmylus*, the spermatophore is eaten by the female (David, 1936) and in *Sialis* it is eventually taken into the bursa, where it is broken up and digested (Khalifa, 1949*b*). Withycombe (1923) describes spermatophores in a number of species and in a later paper (1925) concluded that all of the Neuroptera, except the family Coniopterygidae, produce spermatophores. He further points out that only the Coniopterygidae possess a true penis, by which he presumably means a flagellar structure of some sort.

This family is aberrant in other respects and possibly represents a divergence from the main Neuropteran group (Imms, 1957).

7. THE HYMENOPTERA

There have been insufficient observations to permit any general statement to be made about the Hymenoptera, but in every species that has been examined a spermatophore has been found. Thus, typical spermatophores with sperm sacs and a gelatinous matrix have been found in *Pimpla* (Khalifa, 1949*b*) and various parasitic species (Flanders, 1934 ; 1945).

Other species, however, possess a spermatophore which has been considerably reduced. *Nematus* has lost the sperm sacs, leaving a gelatinous mass resembling the spermatophore of *Rhodnius* both in structure and method of formation (D'Rozario, 1940). Bishop (1920), Laidlaw (1944) and many others have described a copulatory plug in the honey bee consisting of mucus originating in the male accessory glands and supposedly functioning to prevent the backflow of semen after copulation. Although Khalifa (1949*b*) does not consider this to be a spermatophore, there can be little doubt that Fyg (1950) was correct in referring to the structure as one. Khalifa (1948) has described in *Athalia* "a mass of transparent jelly-like secretion" as appearing at the end of copulation in the bursa of the female. He considers that this is not a spermatophore since " it has no definite wall and a mass of sperm tails project from it ". There can be no doubt that this structure is a spermatophore in which the sperm sacs have disappeared ; indeed, the description might be that of the spermatophore in *Rhodnius*.

8. THE COLEOPTERA

Information on the production of spermatophores in the Coleoptera is also very meagre and, at first sight, the distribution of the habit within the order might appear to be more erratic than in the other orders. Muir (1919) was the first to suggest that beetles with a highly developed flagellar intromittent organ do not form spermatophores, while those with a well developed " internal sac " [analogous, perhaps, to the spermatophore sac of *Rhodnius* (Davey, 1959)] would be more likely to do so. Khalifa (1949*b*), however, has pointed out that there are some Coleoptera with no flagellum, but which transfer free sperms. It is possible that these are forms intermediate between the spermatophore-producing forms and those with a flagellum, as has already been noted for Mecoptera.

Khalifa (1949*b*) suggests that the dichotomy between forms producing spermatophores and those delivering free sperms exists within families of the Coleoptera. He cites Cros (1924) as evidence for this statement, claiming that this author found that in both the Tenebrionidae and the Scarabaeidae there were forms which produced spermatophores and those which did not. An examination of the paper in question reveals that Cros, on the basis of fairly extensive evidence, suggested that all of the Tenebrionidae and the Scarabaeidae produced spermatophores. He reached the same conclusion about the Meloidae, but could find no spermatophores in the Cerambycidae or the Curculionidae. In addition, Khalifa (1949*b*) cites *Tenebrio molitor* L. as a tenebrionid which does not form spermatophores, but the present author has found spermatophores in females immediately after copulation. These spermatophores are long and slender, completely filling the tubular bursa copulatrix and consisting of a long sperm sac coiled up in a scanty gelatinous matrix. While it is impossible to make any convincing statement on the basis of scanty evidence, it is clear that the Coleoptera do not present any new problems in the distribution of spermatophores.

9. Conclusion

It is evident from the foregoing that there are large gaps in our knowledge of the distribution of spermatophores in even the major groups of insects, but there is enough information to permit the formulation of a working hypothesis concerning the origin and evolution of the spermatophore habit. It is suggested that the aquatic insect ancestor envisaged by Tiegs (1940) produced an external spermatophore from which the spermatozoa were shed into the water along with the eggs. One of the steps which enabled insects to live on the land was the development of internal fertilization, brought about by the extension of the spermatophore into the female ducts by means of a long neck, with the main part of the spermatophore remaining outside the female. The insect gradually developed a bursa copulatrix as an internal receptacle for the spermatophore.

With the establishment of internal fertilization, the problem facing the insect was that of ensuring that the semen found its way to the spermatheca. Within the insects this problem has resulted in two main trends. One involves the retention of the spermatophore, often in a reduced or modified form, to function as a copulatory plug to hold the semen in place while it is transported to the spermatheca, probably by contractions of the female ducts. The other trend has resulted in the loss of the spermatophore and the development of a more or less elongate penis which transports the semen directly to the spermatheca. This hypothesis assumes that the spermatophores of insects and Onychophora are homologous. A study of the composition of the spermatophores of various species employing the techniques of histochemistry may shed some light on the validity of such an assumption.

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NOTES ON THE HAWKMOTHS (LEPIDOPTERA: SPHINGIDAE) OF NIGERIA

By J. Boorman

Introduction and Acknowledgments

The hawkmoths are one of the most collected families of West African moths, and it is therefore surprising that the literature concerning them should be so scanty. No lists of the Nigerian fauna appear to have been published, except for that of Williams (1954), who operated a light trap at Ibadan, and during a single night captured 60 specimens belonging to 19 species.

These notes are presented in the hope that they may provide a convenient starting point for further study of the Nigerian fauna. Many of the records are based upon a collection formed by the author during the period 1954–59, mainly in the Lagos area. Other sources of records quoted, with the approximate periods covered by the collections, are Williams (*loc. cit.*, 1954), the collections of the British Museum (1900–59) and of University College, Ibadan, Nigeria (1930–59), and the private collections of Mr. E. F. Haig (1930–36) and Dr. B. McNulty (1954–58). To these gentlemen, and to officials of the British Museum and of University College, the author wishes to express his thanks for allowing access to the collections and for much helpful discussion.

The vegetation and climate of Nigeria in relation to the distribution of Tabanidae (Diptera) have been described by Crosskey and Crosskey (1956). Little attempt has been made in the present paper to relate the distribution of species to vegetational or climatic zones, since in most cases the available information represents the distribution of collectors rather than that of the species itself. Much more intensive collecting is needed, particularly in Northern Nigeria, before definite conclusions can be drawn from distribution data.

Again, little is known of the seasonal distribution of the species. The records quoted here are for adult insects actually captured and are drawn from all sources. It is possible, however, that species which occur in different climatic zones may have different seasonal distributions in each zone. For instance, the onset of the rainy season is usually later in savannah areas than in the high forest of Southern Nigeria, and this may modify the time of appearance of a species. The available records, however, are so few that no attempt has been made to analyse them in this manner. Many species have been recorded for almost every month of the year; in these cases systematic collecting with statistical analysis of the results would be needed before any definite conclusion regarding seasonal distribution could be drawn.

Four species occurring in Nigeria are also represented in the British fauna, as rare migrants: they are *Herse convolvuli* L., *Acherontia atropos* L., *Deilephila nerii* L. and *Hippotion celerio* L.

Notes on the Species

Seasonal distribution records are given in brackets after the specific name, the various months being denoted by numerals—5, for example, for the month of May. Sources of locality records are denoted as follows: *BM*, British Museum (Nat. Hist.); *H*, E. F. Haig collection; *I*, University College, Ibadan, collection; *JB*, author's collection; *M*, Dr. B. McNulty's collection; and *W*, Williams (1954). Observations regarding the frequency of occurrence of a species in the Lagos area are based on the author's experience in five year's collecting, but have no strictly numerical basis.

1. *Herse convolvuli* L. (4, 5, 6, 7, 9, 10, 11). Recorded from numerous localities throughout Northern, Eastern, and Western Nigeria. Very common in Lagos. The larvae have been found on Convolvulaceae (*Ipomea* sp.).

PROC. R. ENT. SOC. LOND. (A) 35. PTS. 7–9. OCTOBER 1960.

2. *Acherontia atropos* L. (5, 6, 7, 8, 9, 12). Widely distributed; as in the preceding species, records from all parts of Nigeria. The larvae have been found on *Clerodendron* sp. (known locally as the "pagoda flower").

3. *Coelonia fulvinota* Butler (4, 5, 6, 7, 8, 9, 11). Common in all parts of Nigeria. The larvae feed on *Clerodendron* sp.

4. *Xanthopan morgani* Walker (4, 6, 8, 10, 11). Recorded from Asaba (*BM*), Ilesha (*BM*), Kano (*BM*), Lagos (*JB*) and Sobo (*M*). Rather infrequent in Lagos.

5. *Pemba jordani* Joicey and Talbot (6, 7). Rare; two specimens only, both from Lagos (*JB*). These seem to be the first Nigerian records.

6. *Rhadinopasa hornimanni* Druce (1, 4, 6, 7). Akri Ngida (*BM*), Ikom (*I*), Mamfe (*I*), Port Harcourt (*JB, M*). Possibly a species found more to the east of the Niger than to the west.

7. *Libyoclanis bicolor* Rothschild (6, 7, 9). Records from Ibadan (*BM*), and Lagos (*JB*). In the latter locality occasional, at light.

8. *Libyoclanis major* Rothschild and Jordan (2, 6, 7, 12). One female from Lagos, taken at light by Dr. Roche, and a short series of bred males from Port Harcourt (*Dr. McNulty*). The British Museum contains one specimen labelled "Sierra Leone"; the Lagos specimen corresponds exactly to this and also to the figure, in Seitz (1930), of *Phylloxiphia formosa* Schultze. The type of *P. formosa* was not examined, but it would appear likely that *P. formosa* is merely the female of *L. major*, as suggested in the text of Seitz (*loc. cit.*).

9. *Libyoclanis vicina* Rothschild and Jordan (8). One specimen labelled "Cross River" (*BM*); also one at Lagos (*JB*).

10. *Pseudoclanis postica* Walker (2, 4, 6, 7, 8, 9, 10, 11). Recorded from Afikpo (*H*), Ibadan (*BM*), Ilesha (*BM*), Ilobi (*JB*), Lagos (*JB*), Ogoja (*H*), Okundi (*H*) and Port Harcourt (*M*). This species is represented in Nigeria by the form *occidentalis* R. and J.

11. *Platysphinx constrigilis* Walker (1, 3, 5, 6, 7, 9, 10, 11, 12). Specimens from Adiabo (*BM*), Calabar (*BM*), Cross River (*BM*), Ikom (*I, H*), Ilesha (*BM*), Lagos (*JB*), Port Harcourt (*M*) and Sobo (*M*). Occasional at light in Lagos.

12. *Platysphinx phyllis* Rothschild and Jordan (2, 4, 6, 7, 11, 12). Recorded from Abakaliki (*H*), Enugu (*H*), Ibadan (*H*), Lokoja (*BM*), Ogoja (*H*) and Uwet (*I*). Williams records the closely related *P. piabilis* from Ibadan. That species, however, is characteristically a South African one, and the record may be an error for *P. phyllis*.

13. *Platysphinx stigmatica* Mabille (5, 7, 8). From Port Harcourt only (*M*).

14. *Leucophlebia afra* Karsch (6, 7, 9). Specimens recorded from Abakaliki (*H*), Afikpo (*BM*), Amara (*BM*), Baro (*BM*), Bauchi (*BM*), Enugu (*H*), Ilorin (*BM*), Lagos (*BM*) and Lokoja (*BM*). This species, which is represented in Nigeria by the form *edentata* R. and J., would appear to be characteristic of savannah and more northern areas.

15. *Polyptychus digitatus* Karsch (9). Recorded only from Ibadan (*BM*) and Lagos (*JB*). In the latter locality one specimen only.

16. *Polyptychus virescens* Butler (3, 5, 6, 7, 8, 9, 11). Recorded from Ibadan (*BM*), Ikom (*H*), Ilesha (*BM*), Lagos (*JB*), Obubra (*I*) and Port Harcourt (*M*). Fairly common; not as rare as suggested in Seitz (1930).

17. *Polyptychus trisecta* Aurivillius. One specimen in the British Museum is labelled simply "Nigeria". No others seem to have been recorded from that country.

18. *Polyptychus orthographus* Rothschild and Jordan (1, 2, 4, 6, 7, 8, 9, 10, 12). From Calabar (*BM*), Ilesha (*BM*), Lagos (*JB*), Port Harcourt (*M*) and Sobo (*M*). In the Lagos area, fairly common.

19. *Polyptychus poliades* Rothschild and Jordan (1, 4, 5, 6, 7, 8, 9, 11). From Ibadan (*BM, H, W*), Lagos (*JB*) and Port Harcourt (*M*). One of the commonest species in the Lagos area.

20. *Polyptychus carteri* Butler (2, 3, 4, 5, 6, 7, 8, 9, 11, 12). Recorded from Abakaliki (*H*), Ibadan (*BM*, *H*, *W*), Lagos (*JB*), Obubra (*I*), Olokemeji (*BM*), Port Harcourt (*M*), Sapele (*BM*) and Sobo (*M*). In the Lagos area, very common.

21. *Polyptychus murinus* Rothschild (3, 6, 9). Recorded from Lagos (*JB*) and Port Harcourt (*M*).

22. *Polyptychus cymatodes* Rothschild and Jordan (6). Lagos (*JB*), one specimen only, at light.

23. *Polyptychus rhadamistus* F. (4, 5, 6, 7, 8, 9, 11). Recorded from Agberi (*BM*), Ibadan (*W*), Ikom (*I*), Lagos (*JB*), Onitsha (*BM*) and Sobo (*M*). Common in the Lagos area.

24. *Polyptychus andosus* Walker (3, 5, 6, 7, 12). Recorded from Iju (*JB*), Port Harcourt (*M*) and Sobo (*M*).

25. *Polyptychus anochus* Rothschild and Jordan (6, 11). Lagos (*JB*), two specimens only; these appear to be the only Nigerian records.

26. *Polyptychus consimilis* Rothschild and Jordan (3, 4, 5). Recorded from Jebba (*BM*) and Enugu (*H*). This may possibly be a savannah species.

27. *Polyptychus roseus* Druce (3, 4, 5, 6, 7, 8, 9, 10, 11, 12). Recorded from Abakaliki (*H*), Ibadan (*BM*), Enugu (*H*), Ilesha (*BM*), Ilobi (*JB*), Kaduna (*BM*), Lagos (*JB*), Port Harcourt (*M*) and Sobo (*M*). A common species around Lagos.

28. *Polyptychus foliaceus* Rothschild and Jordan. Apparently one record only, from Kaduna (*BM*).

29. *Polyptychus contrarius* Walker (2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12). Recorded from, and apparently common in, a number of localities; Abakaliki (*H*), Enugu (*H*), Ibadan (*BM*, *H*), Idanre (*JB*), Ikom (*I*), Kaduna (*M*), Lagos (*JB*), Ogoja (*H*), Port Harcourt (*M*). Represented in Nigeria by the form *submarginalis* Walk.

30. *Polyptychus retusus* Rothschild and Jordan (4, 6, 8, 9, 10). Recorded from Ibadan (*W*, *BM*), Ilesha (*BM*), Lagos (*JB*) and Mamfe (*I*).

31. *Polyptychus spurelli* Rothschild and Jordan (9). From two localities only, Calabar (*BM*, *I*) and Ikom (*BM*).

32. *Polyptychus nigriplaga* Rothschild and Jordan (6, 7, 8, 11, 12). From Abakaliki (*H*), Ibadan (*H*), Lagos (*JB*) and Port Harcourt (*M*).

33. *Polyptychus pauperculus* Holland (3, 4, 5, 6, 7, 8, 12). This species is probably widespread throughout Southern Nigeria, as shown from the records: Agberi (*BM*), Calabar (*BM*), Ilesha (*BM*), Lagos (*JB*), Lokoja (*BM*), Obudu (*H*), Onitsha (*BM*), Port Harcourt (*M*), Sapele (*BM*), Sobo (*M*) and Warri (*BM*).

34. *Polyptychus hollandi* Rothschild and Jordan (4). Recorded from Oloibiri (*JB*), Sapele (*BM*) and Warri (*BM*).

35. *Polyptychus molitor* Rothschild and Jordan (7, 11, 12). From Boro (*BM*), Enugu (*H*), Ilorin (*BM*) and Ogoja (*H*). This may well be a savannah species.

36. *Lycosphingia hamata* Dewitz (7, 8, 11). Apparently only three specimens recorded from Nigeria: two from Lagos (*JB*) and one from Sobo (*M*). Presumably rare.

37. *Typhosia illustris* Rothschild and Jordan (3, 4, 8, 10, 11, 12). Recorded from Ikom (*BM*, *I*), Port Harcourt (*M*) and Sobo (*M*).

38. *Acanthosphinx gussfeldti* Dewitz (3, 4, 6, 7, 9, 11). Recorded from Calabar (*BM*), Lagos (*JB*) and Port Harcourt (*M*). Fairly common in Lagos. This species possesses a very strong, characteristic odour, which can be perceived even when the insect is in flight. The enormous spines on the hind tibiae are capable of inflicting a painful wound if the living insect is handled carelessly.

39. *Lophostethus demolini* Angas (3, 4, 5, 6, 8, 9, 10). Represented ln Nigeria by the form *carteri* Rothsch. Recorded from Abakaliki (*H*), Ibadan (*W*), Ilobi (*JB*), Lagos (*JB*), Obudu (*H*), Port Harcourt (*M*), Sobo (*M*) and Zaria (*BM*).

40. *Cephonodes hylas* L. Represented in Nigeria by the form *virescens* Wallengren. Recorded from Ibadan (*I*), Kano (*M*), Lagos (*BM*, *JB*), Minna (*BM* and Port)

Harcourt (*M*). Dr. McNulty has observed that freshly emerged specimens have a covering of loose, greenish scales on the wings, which are lost during the first flight of the insect. The moth is a day flier, usually taken hovering over flowers in bright sunshine.

41. *Deilephila nerii* L. (2, 4, 5, 6, 7, 9). From numerous localities in West, East and North Nigeria. In Lagos, a very common species. The larvae have been found feeding on *Allamanda* sp. and *Rauwolfia* sp.

42. *Nephele vau* Walker. Recorded only from Bauchi (*BM*).

43. *Nephele comma* Hopff (1, 2, 5, 6, 7, 8, 10, 11, 12). Both the nominotypical form and the form *derasa* R. and J. occur in Nigeria. Recorded from Abakaliki (*H*), Calabar (*BM*), Ikom (*I*), Lagos (*JB*), Ogoja (*H*), Onitsha (*BM*) and Port Harcourt (*M*). This species, together with *N. funebris*, *N. peneus* and *N. accentifera*, may be taken freely at dusk hovering over the flowers of the Flamboyant, or Flame tree.

44. *Nephele funebris* F. (1, 4, 5, 6, 9, 10). Recorded from Abakaliki (*H*), Calabar (*BM*), Ibadan (*W*), Ikom (*I*), Lagos (*JB*), Ogoja (*H*) and Port Harcourt (*M*).

45. *Nephele maculosa* Rothschild and Jordan (12). Recorded from Calabar (*BM*) and Port Harcourt (*M*).

46. *Nephele bipartita* Butler (5, 12). Recorded from Calabar (*BM*), Ikom (*I*), Ilesha (*BM*) and Lagos (*JB*). In the Lagos area, infrequent.

47. *Nephele discifera* Karsch (3, 4, 6, 7). From Ikom (*BM*), Lagos (*JB*), Port Harcourt (*M*) and Sobo (*M*). Infrequent in the Lagos area.

48. *Nephele peneus* Cramer (4, 5, 6, 8, 9, 10, 11). Recorded from Bauchi (*BM*), Calabar (*BM*), Enugu (*H*), Ibadan (*W*), Ikom (*I*), Lagos (*BM*, *JB*), Ogoja (*H*), Onitsha (*BM*), Port Harcourt (*M*) and Sapele (*BM*). A very common species. Two specimens were bred in which the stigma of the fore wings was brown instead of the usual white, together with three typical specimens, from five eggs found on an unidentified creeper at Ilobi.

49. *Nephele accentifera* Beauvois (2, 3, 4, 5, 6, 7, 8, 9, 11). Recorded from Abakaliki (*H*), Ahoada (*I*), Ibadan (*H*, *JB*), Lagos (*JB*), Obudu (*H*), Ogoja (*H*), Port Harcourt (*M*) and Sobo (*M*). A very common species.

50. *Nephele rosae* Butler (1, 2, 3, 5, 7, 9, 10, 11, 12). Recorded from Abakaliki (*H*), Calabar (*BM*), Ikom (*I*), Ilesha (*BM*), Ogoja (*H*), Onitsha (*BM*), Port Harcourt (*M*), Sapele (*BM*) and Sobo (*M*).

51. *Nephele aequivalens* Walker (2, 3, 4, 5, 6, 7, 8, 11). Recorded from Abakaliki (*H*), Ibadan (*W*), Lagos (*JB*), Okundi (*I*) and Port Harcourt (*M*). Fairly common in the Lagos area.

52. *Temnora livida* Holland (6, 7, 8, 11). From Calabar (*BM*), Ilesha (*BM*), Lagos (*JB*) and Sapele (*BM*).

53. *Temnora stevensi* Rothschild. One specimen in the British Museum from Ilesha. This is apparently the only Nigerian record.

54. *Temnora funebris* Holland (1, 3, 4, 6, 7, 8, 11). Recorded from Calabar (*BM*), Lagos (*BM*, *JB*), Port Harcourt (*M*) and Sobo (*M*). A fairly common species in Lagos.

55. *Temnora fumosa* Walker (1, 2, 4, 5, 6, 7, 8, 12). Recorded from Abakaliki (*H*), Calabar (*BM*), Enugu (*H*), Ibadan (*H*, *W*), Ikom (*I*), Lagos (*JB*), Port Harcourt (*M*) and Sobo (*M*).

56. *Temnora sardanus* Walker (1, 4, 6, 7, 8, 9). Recorded from Ibadan (*W*) and Lagos (*JB*). Occasional in Lagos.

57. *Temnora atrofasciata* Holland. One specimen only in the British Museum, labelled simply " Nigeria ".

58. *Temnora hollandi* Clark (3). Two specimens only; one from Ibadan (*BM*) and one from Sobo (*M*).

59. *Temnora spiritus* Holland (4, 5, 6, 8). Recorded from Ibadan (*BM*, *W*), Ilesha (*BM*), Lagos (*BM*, *JB*), Sapele (*BM*), Sobo (*M*) and Warri (*BM*).

60. *Temnora elegans* Rothschild (4, 5, 6, 7). Recorded from Abakaliki (*H*) and Ibadan (*W*).

61. *Temnora crenulata* Holland (5, 6, 7, 8, 9). Recorded from Lagos (*BM*, *JB*) and Sobo (*M*). Fairly common in the Lagos area.

62. *Temnora reutlingeri* Holland. One specimen only, from Calabar (*BM*).

63. *Temnora scitula* Holland (1, 3, 6, 7, 8, 11). Recorded from Lagos (*JB*) and Sobo (*M*).

64. *Temnora eranga* Holland. One record only, from Ilesha (*BM*).

65. *Temnora iapygoides* Holland (1, 3, 5, 6, 7, 8, 9). Recorded from Enugu (*H*), Ikom (*H*), Lagos (*BM*, *JB*) and Sobo (*M*). Fairly common in the Lagos area.

66. *Pseudenyo benitensis* Holland (5, 11). Recorded from Ibadan (*H*), Lagos (*JB*) and Port Harcourt (*M*).

67. *Sphingonaepiopsis nana* Boisduval (3, 4, 5, 6, 12). Recorded from Ikom (*I*), Ilobi (*JB*), Lagos (*JB*), Port Harcourt (*M*) and Sobo (*M*). Common in the Lagos area ; usually taken hovering over flowers at dusk.

68. *Antinephele anomala* Butler (3, 4, 6, 7, 8, 12). Recorded from Ikom (*H*), Ilesha (*BM*), Lagos (*BM*, *JB*), Obubra (*I*), Port Harcourt (*M*) and Sobo (*M*).

69. *Antinephele achlora* Holland (1). One specimen only, from Sobo (*M*).

70. *Antinephele muscosa* Holland (1). One specimen only, from Sobo (*M*).

71. *Antinephele lunulata* Rothschild and Jordan. One specimen only, from Lagos (*BM*). This and the preceding two species are presumably rare.

72. *Antinephele maculifera* Holland. One record only, from Lagos (*BM*).

73. *Hypaedalia butleri* Rothschild (7, 11). Recorded from Ibadan (*BM*), Ikom (*H*, *BM*), Ilesha (*BM*) and Uwet (*I*).

74. *Hypaedalia insignis* Butler (12). Recorded from Ilesha (*BM*) and Lagos (*BM*, *JB*). Only one specimen taken by the author, from Lagos.

75. *Atemnora westermanni* Boisduval (1, 2, 3, 4, 6, 8, 10, 11). Recorded from Abak (*I*), Abakaliki (*H*), Ibadan (*W*), Lagos (*JB*), Mamfe (*I*), Ogoja (*H*), Olokemeji (*H*), Port Harcourt (*M*) and Sobo (*M*).

76. *Macroglossum trochilus* Hübner (1, 5, 6, 7). Many specimens in the British Museum from the following localities: Baro, Bauchi, Calabar, Ikot-Ekpenne ; Ilesha, Lokoja, Minna and Mount Cameroon. Also recorded from Abakaliki (*H*), Lagos (*JB*) and Ogoja (*H*). A day flier.

77. *Leucostrophus commasiae* Walker (3, 5, 9). Recorded from Abakaliki (*H*), Lagos (*Dr. Roche*), Ogumni (*BM*) and Oringa (*BM*). Another day flier.

78. *Euchloron megaera* L. (1, 6, 8, 9, 11, 12). Recorded from Lagos (*JB*), Port Harcourt (*M*) and Sobo (*M*). Common in the Lagos area.

79. *Basiothea medea* Felder (3, 5, 6, 8, 9, 10, 11). Recorded from Ikom (*H*, *JB*), Ilorin (*JB*), Lagos (*JB*), Port Harcourt (*M*) and Sobo (*M*). Common in the Lagos area. Is attracted to flowers at dusk and to light later in the evening.

80. *Basiothea charis* Boisduval (1, 3, 11, 12). Recorded from Ikom (*H*, *I*), Lagos (*JB*) and Sobo (*M*). An uncommon species in Lagos.

81. *Hippotion osiris* Dalman (1, 3, 4, 5, 6, 7, 8, 9, 12). Recorded from Abakaliki (*H*), Ibadan (*W*), Ikom (*H*), Lagos (*JB*), Ogoja (*H*), Onitsha (*I*) and Port Harcourt (*M*). A common species.

82. *Hippotion celerio* L. (2, 3, 4, 5, 6, 7, 9, 10, 11). Recorded from Ibadan (*H*, *W*), Ikom (*H*, *I*), Lagos (*JB*), Ogoja (*H*) and Port Harcourt (*M*). A common species.

83. *Hippotion eson* Cramer (1, 2, 4, 5, 6, 7, 8, 9). Recorded from Abakaliki (*H*), Agwa (*I*), Ibadan (*W*), Lagos (*JB*), Port Harcourt (*M*) and Sobo (*M*). A common species.

84. *Hippotion balsaminae* Walker (1, 5, 6, 7, 8, 9, 10, 11, 12). Recorded from Ibadan (*H*), Lagos (*JB*) and Port Harcourt (*M*). A common species.

85. *Hippotion irregularis* Walker (1, 2, 3, 4, 5, 6, 10, 12). Recorded from Agberi

(*BM*), Asaba (*BM*), Ibadan (*Caswell*), Ilobi (*JB*), Kumba (*JB*), Port Harcourt (*M*), Sobo (*M*) and Warri (*BM*).

86. *Theretra jugurtha* Boisduval (6, 7, 9). From Lagos only (*JB*), occasional.

87. *Theretra cajus* Cramer. From Olokemeji (*BM*), no other records.

88. *Theretra orpheus* Herrich-Schaeffer (5, 6, 8, 12). Recorded from Ibadan (*BM*), Lagos (*JB*) and Port Harcourt (*M*).

89. *Centroctena rutherfordi* Druce (1, 4, 5, 8, 9, 12). Recorded from Calabar (*BM*), Enugu (*H*), Ilesha (*BM*), Lagos (*JB*) and Port Harcourt (*M*).

In addition to the above, two other species have been recorded, but have not yet been determined. One, a female *Polyptychus*, was taken at Ibadan (*JB*), and the other, a *Temnora* sp., has been taken at Lagos (*JB*, one specimen) and Port Harcourt (*Dr. McNulty*, a short series). This brings the number of records of Nigerian Sphingidae species known to the author to 91.

LIST OF LOCALITIES MENTIONED

Map references have been taken from 1 : 500,000 road maps published by the Survey Department, Lagos (1953). Rainfall data have been obtained from figures published by the Meteorological Department, Lagos, and represent mean annual rainfall in inches for periods of not less than five years, to the nearest inch. Approximate altitudes and vegetational zones are from maps contained in the *Nigeria Handbook* (1954). The following abbreviations have been used : *FWS*, Fresh water swamp ; *GS*, Guinea savannah ; *M*, Mangrove swamp ; *Mont*, Montane ; *RF*, Rain forest ; *SS*, Sudan savannah.

Locality	Latitude (deg. north)	Longitude (deg. east)	Approx. altitude	Rainfall (inches)	Vegetation zone
Abak	4.58	7.47	<500	93	*RF*
Abakaliki	6.19	8.06	<500	83	*GS*
Adiabo		Southern Nigeria, unidentified.			
Afikpo	5.54	7.56	<500	79	*GS*
Agberi	5.17	6.23	<500	95	*FWS*
Agwa		? Eastern Nigeria, unidentified.			
Ahoada	5.06	6.39	<500	98	*FWS*
Akri Ngida	5.45	6.37	<500	80	*RF*
Amara		? Northern Nigeria, unidentified.			
Asaba	6.12	6.43	<500	64	*RF*
Baro	8.35	6.18	<500	55	*GS*
Bauchi	10.18	9.48	2300	43	*SS*
Boro			See Baro.		
Calabar	4.57	8.20	<500	125	*M*
Enugu	6.27	7.29	750	73	*GS*
Ibadan	7.23	3.50	700	50	*RF*
Idanre	7.07	5.06	1,700	48	*RF*
Iju	6.41	3.18	<500	54	*RF*
Ikom	5.58	8.42	<500	98	*RF*
Ikot-Ekpenne	5.10	7.42	<500	92	*RF*
Ilesha	7.37	4.44	1,200	52	*RF*
Ilobi	6.45	3.02	<500	53	*RF*
Ilorin	8.30	4.32	1,300	50	*GS*
Jebba	9.07	4.48	<500	45	*GS*
Kaduna	10.32	7.28	1,900	51	*GS*
Kano	12.02	8.32	1,500	34	*SS*
Kumba	4.38	9.25	800	91	*RF*
Lagos	6.20	3.20	<500	70	*RF*
Lokoja	7.48	6.44	<500	50	*GS*

Locality	Latitude (deg. north)	Longitude (deg. east)	Approx. altitude	Rainfall (inches)	Vegetation zone
Mamfe . .	5.47	9.17	<500	134	*RF*
Minna . .	9.37	6.32	850	53	*GS*
Mt. Cameroon .	4.13	9.11	13,350	200	*Mont*
Ngida . .		See Akri Ngida.			
Obubra . .	6.06	8.20	<500	79	*GS*
Obudu . .	6.38	9.07	700	68	*GS*
Ogoja . .	6.35	8.45	750	73	*GS*
Ogumni . .		? Northern Nigeria, unidentified.			
Okundi . .	6.25	8.42	1,200	73	*GS*
Oloibiri . .	4.41	6.22	<500	96	*M*
Olokemeji . .	7.27	3.31	<500	48	*RF*
Onitsha . .	6.10	6.47	<500	76	*RF*
Oringa . .		? Southern Nigeria, unidentified.			
Port Harcourt .	4.51	7.01	<500	94	*RF*
Ropp . .		? Northern Nigeria, unidentified.			
Sapele . .	5.54	5.42	<500	100	*FWS*
Sobo (Sobo Plain)	5.46	5.49	<500	100	*RF*
Uwet . . .	5.16	8.12	<500	125	*M*
Warri . .	5.31	5.43	<500	109	*FWS*
Zaria . . .	11.07	7.43	2,000	44	*GS*

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SOME RECORDS OF DIPTEROUS AND HYMENOPTEROUS PARASITES OF TSETSE FLY PUPAE[1]

By D. S. Saunders[2]

(From the Department of Entomology, London School of Hygiene and Tropical Medicine)

During a laboratory investigation into the biology of the *Syntomosphyrum* parasites of tsetse flies 5,000 pupae of *Glossina morsitans* Westwood were received from Tanganyika, and 2,609 pupae of *G. pallidipes* Austen, together with a smaller number of *G. brevipalpis* Newstead and *G. longipennis* Wiedemann, were received from Kenya. Besides *Syntomosphyrum* several other parasites emerged from these pupae and it is thought that the following records may be of interest.

1. *Syntomosphyrum* spp. (Hymenoptera : Eulophidae)

Two species of this genus (*S. glossinae* Waterston and *S. albiclavus* Kerrich) emerged from *Glossina* pupae. *Syntomosphyrum glossinae* was obtained from three (0·11 per cent.) of the 2,609 *G. pallidipes* pupae collected in Kiboko and Makueni, Kenya, between July 1957 and March 1958, but it was not recorded from *G. morsitans*. *Syntomosphyrum albiclavus* is a new species described by Kerrich (1960). The known distribution and biological evidence for the separation of this species, which differs from *S. glossinae* in that the female has white-clubbed antennae, is given by Saunders (1960). Five (0·10 per cent.) of the 5,000 *G. morsitans* pupae collected at Singida, Tanganyika, between October 1956 and December 1957 produced broods of this chalcid. It was also obtained from one pupa of *G. pallidipes* collected at Kiboko, Kenya, in September 1957. The parasitization rates quoted here are rather lower than those recorded for *S. glossinae* by Lamborn (1925) in Nyasaland and by Nash (1933) in Tanganyika.

The *G. pallidipes* pupa and the *G. morsitans* pupae parasitized by *S. albiclavus* were all collected between the months of September and early June. The three *G. pallidipes* pupae parasitized by *S. glossinae* were collected during September and October. Neither of these species of *Syntomosphyrum* emerged from pupae collected between July and early September (during the long dry season), so that there would seem to be some evidence that the incidence of these chalcids in tsetse pupae is seasonal. A similar seasonal emergence was also noted in Southern Rhodesia by Chorley (1929), who recorded the greatest incidence of *S. glossinae* in *G. morsitans* pupae collected between September and November.

None of the 188 *G. brevipalpis* or the 169 *G. longipennis* pupae from Kenya were parasitized by *Syntomosphyrum*.

2. *Stomatoceras micans* Waterston (Hymenoptera : Chalcididae)

Six *S. micans* emerged from the *G. pallidipes* pupae collected in Kenya, a parasitization rate of 0·23 per cent. Of these six specimens, one emerged from a batch of 102 pupae collected at Lower Makueni and five came from a single batch of 345 pupae from Kiboko. One specimen of this chalcid was also bred from *G. morsitans* sent from Singida.

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[1] This paper is part of a thesis for the Ph.D. degree, University of London, submitted October, 1958.

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3. *Thyridanthrax* spp. (Diptera : Bombyliidae)

The three species of *Glossina* from Kenya were all parasitized by three species of *Thyridanthrax* : *T. abruptus* Loew, *T. alliopterus* Hesse and *T. lugens* Loew. These flies were the most frequent parasites obtained. Three specimens of *T. abruptus* also emerged from *G. morsitans* collected at Singida.

The taxonomy of this genus has been in dispute, but in the present investigation the monograph of Hesse (1956) was followed. The three species of *Thyridanthrax* obtained were not identified until all the flies had emerged and consequently the details of emergence are for the genus only. The percentage of *Glossina* pupae parasitized by these Bombyliids is shown in Table I. Similar high rates of parasitism by *Thyridanthrax* have been recorded by Parsons (1954) and by Du Toit (1954).

Table I.—*The percentage of* Glossina *pupae parasitized by* Thyridanthrax *spp.*

Species of *Glossina*	Number of pupae	Number of *Thyridanthrax*	Percentage of pupae parasitized by *Thyridanthrax*
G. brevipalpis . .	188	41	21·8
G. pallidipes . .	2609	249	9·5
G. longipennis . .	169	7	4·1

Table II gives an indication of the seasonal nature of parasitism by *Thyridanthrax* spp. in *G. pallidipes* pupae collected in Kenya. The fewest *Thyridanthrax* emerged from those pupae collected during September and October. These are probably either the progeny of flies active during the dry season, or the imagines of diapause larvae. A peak of infection occurred during the period from November to February. No pupae were received between April and June. Chorley (1929), working in Southern Rhodesia, also found that the incidence of these parasites in tsetse pupae was seasonal. In this area, a peak of parasitism by *Thyridanthrax* occurred in November and a low rate of infection between June and September.

Table II.—*The monthly rate of parasitization of* G. pallidipes *pupae from Kenya by* Thyridanthrax *spp.*

Month	Number of pupae	Number of *Glossina* emerged	Number of *Thyridanthrax*	Percentage of pupae parasitized
1957				
July . . .	222	145	27	12·2
August . .	748	423	99	13·2
September . .	392	130	21	5·4
October . .	1052	432	56	5·3
November . .	38	17	10	26·3
December . .	12	0	2	16·6
1958				
February . .	60	15	25	41·7
March . . .	85	66	9	10·6

4. Some Phoridae and Borboridae bred from *Glossina brevipalpis*

In November 1956 some dead *G. brevipalpis* pupae were received from Zululand which were found to be infested with mites and some small Cyclorrhaphous flies. Some of the puparia of these flies were adhering to the inside walls of the empty *Glossina* cases.

The flies were identified as *Megaselia* sp. (Diptera : Phoridae) and a few specimens of *Limosina* sp. (Diptera : Borboridae). Unfortunately the insects were in poor condition and a more accurate identification was not possible. The Phorids did not show any sign of the specialised structures normally associated with parasitism in this group and are considered to be scavengers which had fed on the dead *Glossina* pupae. The Borboridae, a group which are also normally found breeding in decaying organic matter, are also thought to be scavengers.

ACKNOWLEDGMENTS

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A LIST OF ODONATA FROM GHANA, WITH NOTES ON THEIR MATING, FLIGHT AND RESTING SITES

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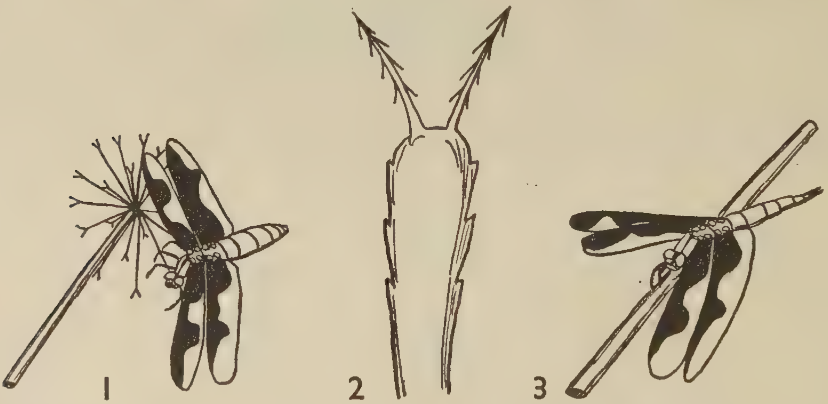
I. Introduction

These notes refer to Odonata collected and determined by the author on the Second Biological Expedition to Ghana, West Africa, sponsored by the Imperial College Exploration Board, during August and September, 1958. Most of the collecting was carried out in the Bobiri Forest Reserve, 23 miles from Kumasi, in Ashanti. For five weeks before our visit there had been drought in the semi-deciduous tropical forest, and during our six weeks' stay we experienced only three short rain storms. The streams and ponds were therefore very low, and many of the ditches, in which several species breed, were almost dry. Several species were therefore only beginning to emerge during the last week of our stay.

II. Biological Notes

Palpopleura lucia f. *lucia* (Drury) and f. *portia* (Rambur) (Libellulidae, Diastatopidinae)

This species was found entrapped in fairly large numbers (10–20 per plant, 4 feet high), on the spiny fruits of a Composite plant in Kumasi. The dragonflies were being killed and eaten by ants. Other species were occasionally found caught in this way (fig. 1), with their bodies affixed to the fruits, but most of the corpses found belonged to *P. lucia*, for which this plant forms a favourite resting perch.



Figs. 1–3.—(1) Corpse of *Palpopleura lucia* attached to Composite fruit (half nat. size); (2) apex of single pappus of Composite; (3) *P. lucia* at rest, showing wings pronated forwards.

This species exhibits a rather unusual resting position, with the wings pronated forwards, in a position similar to that adopted towards the end of the downstroke of the wings in most species (fig. 3).

Hadrothemis infesta Karsch (Libellulidae, Libellulinae)

During oviposition the females hover over the surface of a pond or ditch, about an inch and a half above the water surface, dipping the tip of the abdomen jerkily into the water at intervals of about a second (fig. 4), and releasing a bundle of eggs, which are held before deposition in a manner similar to that adopted by *H. coacta* (fig. 5).

Hadrothemis coacta Karsch (Libellulidae, Libellulinae)

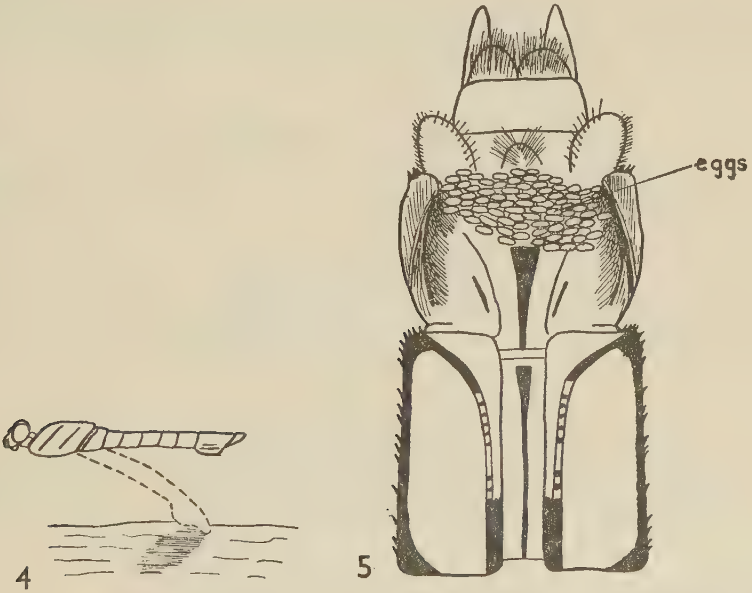
The complete oviposition and mating behaviour of this species was observed as follows :

(1) Male and female approached a pond in the forest.

(2) The female hovered over the water with the male hovering about 12 inches above her.

(3) The male then fluttered his wings with an audible rustle, at the same time shaking his abdomen vigorously from side to side, while continuing to hover over the female.

(4) The female began to use the scoop, formed from the tergites at the end of the abdomen (fig. 5) to scoop drops of water out of the pond; flicking them about 2 feet through the air on to the mud bank (the body action is the same as in *H. infesta*, shown in figure 4). It seems likely, from what is recorded below, that at least one act of mating must have occurred before the start of the observations, and that the scooping process represented oviposition behaviour.



Figs. 4–5.—(4) *Hadrothemis infesta :* lateral view to show oviposition movements of abdomen ; (5) *H. coacta :* ventral view of female abdominal segments 7–10 to show egg scoop on segment 8 (from a specimen captured immediately before oviposition).

(5) The male then descended, flying in a side-to-side manner, grasping the female with a quick movement of the claspers and taking up the mating position.

(6) All the pairs observed then flew off, but were followed by eye and seen to separate and fly back to the pond, repeating the whole process.

(7) While hovering over the female, the male would attack other males flying past, driving them off.

This species therefore exhibits a remarkable degree of manoeuvreability in the air during mating. It is also highly selective in its choice of resting site ; males were observed chasing and supplanting each other on resting perches.

The expansions of the terga of segment 8 in the female also function in holding eggs before deposition. Figure 5 shows the terminalia of a female caught with undeposited eggs.

Hadrothemis camarensis (Kirby) (Libellulidae, Libellulinae)

Mating of this species was observed deep in the forest, about half a mile from any large streams.

Tetrathemis camerunensis Karsch (Libellulidae, Tetratheminae)

This species was observed settled on reeds, along which they crawled about 3 inches before taking off. This observation is of interest because the legs of Odonata are normally used for walking only just after emergence and before wing expansion. This is because the skewness developed in the thorax has moved the wings backwards and the legs forwards (Needham and Anthony, 1903), so that the latter are well adapted for seizing prey in flight but can obtain only a very poor leverage for walking. The length of the abdomen in Odonata also impairs the efficiency of walking.

The mating behaviour of the species was observed to be as follows. The male sits on a twig ; when a female of the same species flies past, he flies quickly towards it, the mating flight position is taken up, and the pair fall into the herbage below. The whole procedure lasts only about five seconds.

Onychogomphus supinus Selys (Gomphidae, Gomphinae)

During the drought this species was observed laying eggs in a puddle in the forest track measuring only 2 feet across.

Pantala flavescens (Fabricius) (Libellulidae, Pantalinae)

This species, which had a large emergence after the day on which rain fell for the first time in several weeks, was observed attempting to oviposit on the surface of a green canvas tent in a clearing.

Trapezostigma limbata (Desjean) (Libellulidae, Pantalinae)

An individual of this species was captured at Kwadaso in the early morning, settled near to an all-night light, to which it had presumably been attracted during the night. The resting position was with the body hanging downwards.

Heliaeshna lanceolata Le Roi (Aeshnidae, Gynacanthaginae)

This species was observed hawking over ponds all through the day until after dusk, and could still be heard when darkness fell. Its activities are therefore not restricted to the crepuscular period, as has been reported for the genus. The characteristic flight includes long spells of hovering in one spot, from 1 to 6 feet above the ground, often for periods of over three minutes. It settles in the normal manner of this family, with the abdomen hanging vertically downwards, and usually chooses resting sites 2–3 feet inside bushes and undergrowth. Two males were observed to settle at different times in a bushy tangle, in exactly the same spot. The species therefore shows some selection of resting site, a phenomenon more normally associated with the Libellulidae. The females were observed ovipositing in the moist soil around the ponds, on which they settled with the body horizontal, another habit peculiar to this family.

Chlorocypha glauca glauca (Selys) (Chlorocyphidae)

The mating flight was observed as follows :

The male flies above the female and in doing so curls the fifth to tenth segments of the abdomen beneath him to display their bright red coloration. (The female abdomen is black and yellow-brown.) Pairing then occurs in the usual manner. The abdomen is also used in an aggressive warning display to other males. Two males hover alongside each other, about one foot apart ; both move forward, maintaining the same relative position ; the attacking male then curls the abdomen at segment 5, exposing the red colour as a warning, and hovers above the other male, finally driving him off by a chasing flight.

This species also shows some choice of resting site, usually settling on a piece of wood close to the water surface. It returns again and again to the same perch when disturbed, as do species of Libellulidae. This habit appears, however, to be uncommon among Zygoptera.

III. LIST OF SPECIES COLLECTED IN ASHANTI, GHANA, WEST AFRICA

Anisoptera

AESHNIDAE

Gynacanthaginae : *Heliaeshna lanceolata* Le Roi

GOMPHIDAE

Gomphinae : *Onychogomphus supinus* Selys

LIBELLULIDAE

Tetratheminae : *Tetrathemis camerunensis* Karsch
    Allorhizuca klingi Karsch
Libellulinae : *Hadrothemis camarensis* (Kirby)
    H. coacta Karsch
    H. infesta Karsch
    Orthetrum julia Kirby
Diastatopidinae : *Palpopleura lucia* f. *lucia* (Drury)
    P. lucia f. *portia* (Rambur)
Brachydiplactinae : *Thermochoria equivocata* Kirby
    Chalcostephia flavifrons Kirby
Sympetrinae : *Acisoma ascalaphoides* Rambur
    A. trifidum Kirby
    Brachythemis leucosticta (Burmeister)
Tritheminae : *Trithemis annulata* (Beauvois)
    T. arteriosa (Burmeister)
    T. pluvialis Förster
    T. nuptialis Karsch
Pantalinae : *Pantala flavescens* (Fabricius)
    Trapezostigma limbata (Desj.)

Zygoptera

CHLOROCYPHIDAE

Chlorocypha glauca glauca (Selys)
C. dispar (Beauvois)
C. selysi (Karsch)

AGRIIDAE

Agriinae : *Sapho bicolor* Selys
S. ciliata (Fabricius)
Phaon iridipennis (Burmeister)

PROTONEURIDAE

Diasparoneurinae : *Chlorocnemis inepta* Grün
Prodasineura villiersi Fraser, n. s. sp. (?)

PLATYCNEMIDAE

Platycneminae : *Platycnemis congolensis* Martin

COENAGRIIDAE

Pseudagriinae : *Ceriagrion suave* Ris
C. glabrum (Burmeister)
C. platystigma Fraser
Pseudagrion thenartum Fraser
P. melanicterum Selys

Finally, the following species collected in Bathurst, Gambia, may also be noted here :

Hemianax ephippiger (Burmeister) (AESHNIDAE)
Hemistigma albipuncta (Rambur) (LIBELLULIDAE)
Trapezostigma basilaris Palisot de Beauvois (LIBELLULIDAE)
Thermochoria equivocata Kirby (LIBELLULIDAE)
Urothemis edwardsi Selys (MACRODIPLACTIDAE)
Ischnura senegalensis Rambur (COENAGRIIDAE)

IV. ACKNOWLEDGMENTS

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V. REFERENCE

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THE SIGNIFICANCE OF QUEEN SUBSTANCE IN SWARMING AND SUPERSEDURE IN HONEY-BEE (*APIS MELLIFERA* L.) COLONIES.

By C. G. Butler
(*Rothamsted Experimental Station*)

Introduction

Butler (1954) obtained results suggesting that the workers of a honey-bee colony do not attempt to rear further queens while they get enough of a particular substance from their queen. Butler and Simpson (1958) found that this *queen substance*, which can be extracted in ethanol from the bodies of queen honey-bees (Butler and Gibbons, 1958), is produced in a queen's mandibular glands, and suggested that during grooming she spreads it over her body, from where her workers obtain it. Butler, Callow and Johnston (1959) obtained a biologically active, crystalline preparation of queen substance which appears to be an $\alpha:\beta$-unsaturated carboxylic acid, containing an unconjugated carbonyl group.

Absence or shortage of queen substance under experimental conditions leads to worker bees rearing queens (Butler, 1954, 1956, 1957); hence too little queen substance may also account for queen rearing in normal colonies, not only after losing the queen but also during preparations for swarming and queen supersedure.

To test this idea attempts were made to measure and compare the quantities of queen substance obtainable from queens of the following types:

(*a*) Mated laying queens heading apparently normal colonies in which no queens were being reared (= mated laying queens).

(*b*) Mated queens that had been superseded by daughter queens, but the mother and daughter queens found still living together (= superseded queens).

(*c*) Mated queens taken from swarms (= swarm queens).

Methods

A standard preparation (1 S.) of queen substance was prepared by extracting 136 mated laying queens in 250 ml. of ethanol, to which was later added a further 90 ml. of ethanol.

Queen substance from individual queens was extracted in 5 ml. ethanol in a micro-Soxhlet apparatus for 48 hours; the resulting solution was called a half-standard (= $\frac{1}{2}$ S.), and a series of dilutions in ethanol was prepared from it for assay.

The method of bioassay used was that of Butler and Simpson (1958), in which 150 worker bees, recently made queenless, are kept at 32° C. in a cage containing food and young female larvae in worker cells. Unless supplied with sufficient queen substance, the bees construct one or more emergency queen cells overnight.

Each cage contained the body of a queen from which all queen substance had been extracted. Control cages contained such fully-extracted queens that had been dipped in ethanol only; other cages contained fully-extracted queens that had been dipped in ethanol extracts of the queen under test. On average each queen removed 0·15 ml. of the solution in which she was dipped; the ethanol was allowed to evaporate before the body of the queen was placed in a cage.

At least 24 cages, of which half were controls, were used in each comparison, and the emergency queen cells were counted 22 hours after the queens' bodies were put in the cages.

Results and Conclusions

Table I gives the results of assays with the standard preparation at different dilutions and shows that the workers detected the queen substance at a dilution of 1/16 S. ($P < 0{\cdot}001$) and possibly at 1/32 S. ($P < 0{\cdot}02$). Table I also gives results of assays on six mated laying queens, seven superseded queens and 11 swarm queens from uncrowded colonies. The results with the six mated laying queens individually extracted did not vary significantly more than did the results of seven tests with the standard preparation made from 136 queens. Although the extracts from superseded and swarm queens from uncrowded colonies contained some queen substance, they were much less effective at $\frac{1}{4}$ S. in preventing queen cell formation than were extracts from mated laying queens. Superseded queens and swarm queens from uncrowded colonies both seem to contain only about one-quarter as much queen substance as do mated laying queens, suggesting that inability of the queen to supply enough queen substance may be the cause of the rearing of queens in uncrowded colonies during swarming preparations just as it is during those for supersedure (Butler, 1957).

Table I.—*Relative amounts of queen substance obtained from various types of queens.* (*Mean number of cages, out of* 12 *in each observation or test, with emergency queen cells. Standard error of each mean in brackets*)

Source of extract	Number of observations	Mean at						
		1 S.	1/2 S.	1/4 S.	1/8 S.	1/16 S.	1/32 S.	*Nil*
Pooled extract of 136 mated laying queens	.	(2 tests) 0·00 (0·00)	(4 tests) 0·00 (0·00)	(7 tests) 0·57 (0·20)	(6 tests) 1·33 (0·33)	(4 tests) 7·75 (0·48)	(5 tests) 10·00 (0·71)	(7 tests) 11·71 (0·18)
Single mated laying queens	6	.	.	0·33 (0·21)	.	.	.	11·17 (0·31)
Single superseded queens	7	.	.	6·28 (0·84)	.	.	.	11·43 (0·20)
Swarm queens from uncrowded colonies	11	.	.	6·18 (0·88)	.	.	.	11·27 (0·27)
Swarm queens from overcrowded colonies	2	.	0·00 (0·00)	0·50 (0·50)	1·50 (0·50)	7·00 (1·00)	.	12·00 (0·00)

Several honey farmers have told me that, when a swarm from an uncrowded colony is hived with its old queen, the workers usually attempt to supersede her within a few weeks, certainly before the new colony reaches a size comparable with that of the parent colony before the swarm was emitted. If this is so an additional factor must determine whether any particular colony will supersede its queen or swarm with her, as Simpson (1958) pointed out. Perhaps, as he suggested, queen substance deficiency induces swarming in large colonies when the environmental conditions favour swarming, and induces supersedure in small or large ones when environmental conditions are unfavourable.

Simpson (1958) showed that in summer colonies can be induced to swarm by overcrowding their bees. Although under such conditions production of queen substance does not decline, its collection probably becomes disorganised and its distribution restricted. There is some direct evidence for this idea: two young mated laying queens obtained from swarms from colonies stated to have been badly overcrowded were extracted and assayed: each had an amount of queen substance not significantly different from an average mated laying queen from a colony not rearing queens, and each had significantly more at $\frac{1}{4}$ S. than swarm queens from colonies stated to have been uncrowded ($P < 0{\cdot}03$) (Table I).

Workers may fail to obtain enough queen substance when overcrowded because of increased demand rather than failure of distribution. No satisfactory way of testing distribution has been devised but the possibility of increased demand was investigated by comparing the abilities of $\frac{1}{4}$ S. and $\frac{1}{8}$ S. levels of queen substance (from the same source as that used in Table I—pooled extract of 136 queens) to inhibit queen rearing by groups of bees from colonies in which no queens were being reared and by groups from crowded colonies in which many queens were being reared before swarming. Table II shows there was no significant difference in the ability of the extract at the levels used to inhibit queen rearing by bees from swarming and from non-swarming colonies, so it is unlikely that their queen substance requirements differ.

TABLE II.—*The abilities of* 1/4 *S. and* 1/8 *S. extracts of mated laying queens to inhibit queen rearing by workers from swarming and non-swarming colonies. Bees from* 3 *swarming and* 3 *non-swarming colonies.* (*Mean number of cages, out of* 12 *in each observation, with emergency queen cells. Standard error of each in brackets*)

	Number of observations	Mean at		
		1/4 S.	1/8 S.	*Nil*
Swarm bees . . .	3	0·67 (0·33)	1·33 (0·88)	11·00 (0·58)
Non-swarm bees . .	3	1·00 (0·58)	1·67 (0·33)	11·00 (0·58)

It is concluded : (*a*) that queen rearing by an uncrowded colony during swarming or queen supersedure preparations is caused by the queen failing to produce enough queen substance, (*b*) that queen rearing during swarming preparations in an overcrowded colony is not necessarily caused by the queen producing too little substance but probably by the substance being collected and distributed inefficiently, (*c*) that evidence is inadequate to show why a colony sometimes supersedes its queen when she produces too little queen substance and at other times swarms with her.

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SUMMARY

(1) Measurements have been made of the quantities of queen substance obtainable from (*a*) mated laying queens from colonies without queen cells, (*b*) superseded queens, (*c*) mated queens from swarms from both uncrowded and overcrowded colonies.

(2) Both superseded and swarm queens from uncrowded colonies contained about one-quarter as much queen substance as the mated laying queens : swarm queens from overcrowded colonies had about as much as the mated laying queens.

(3) The demand for queen substance by workers from colonies preparing to swarm is no greater than that by workers from non-swarming colonies.

(4) It appears that queen rearing by uncrowded colonies preparing to supersede their queen or to swarm with her is caused by the queen producing too little queen substance, but that queen rearing in an overcrowded colony before swarming is not necessarily due to inadequate production of queen substance but could be due to its inefficient collection and distribution.

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